Burning for birds: The response of bird communities to recent fire history in the Serengeti ecosystem

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Minor dissertation presented in partial fulfillment of the requirements for the degree of Master of Science in Conservation Biology in the Department of Biological Sciences,

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Submitted: February 2014

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Plagiarism declaration

I know the meaning of plagiarism and declare that all of the work in the dissertation, save for that which is properly acknowledged, is my own.

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Abstract

Fire is a ubiquitous ecosystem process with important implications for savanna ecology and conservation. In this study we aimed to explore the short-term and long-term effects of recent fire history on bird communities in the greater Serengeti savanna ecosystem in Tanzania. The study investigated the influence of immediate fire event history (< one year), cumulative fire regime history (over 14 years), and fire seasonality on bird assemblages. We predicted that the occurrence of recent fire events and cumulative fire regime history would influence bird communities, particularly through its impact on vegetation structure.

We mapped fire activity from remote sensing data (2000-2013) and extracted mean rainfall and nitrogen estimates from interpolated maps. We conducted field sampling of bird community composition and vegetation structure at 207 sample sites distributed across the western Serengeti ecosystem. We tested the structuring effect and regression trends of recent fire event occurrence, cumulative fires regimes, rainfall, and nitrogen on bird community structure and vegetation, and tested the response of birds to vegetation.

Despite a high degree of variation in bird communities and vegetation structure, our results suggested that fire regimes do indeed impact bird communities with important conservation implications. We detected the strongest changes in bird community structure, diversity, and density in response to the immediate impact of a fire event and post-fire regeneration processes, and weaker effects to cumulative fire regime history. Short fire season burning (Feb-April) appears to have significant influence on birds and vegetation structure, and these preliminary findings warrant further investigation. While

our findings do not have alarming conservation implications, the effects of seasonality and frequency of fires are not negligible. We recommend against extensive burning practices over short periods to allow continuity in the landscape. We recommend greater forethought among conservation managers, bearing in mind both short-term and long-term habitat changes caused by burning and the consequent bird assemblages impacted. We advise focused research on species and functional groups of conservation interest.

Acknowledgements

I am deeply grateful to my supervisor Dr. Colin Beale for his dedicated support, from the initial invitation to work in Tanzania under the Serengeti Fire Project, through planning, fieldwork, data analyses, and writing. I could not have hoped for a more engaged and responsive supervisor. Likewise, I am sincerely thankful to my UCT supervisor Prof. William Bond for sharing his wealth of knowledge and ecological insight particularly in the initial planning and final writing stages.

Given the funding requirements for carrying out wildlife research in remote parts of the Serengeti ecosystem, I am profoundly grateful to my supervisors for support through their respective departments. I am also thankful to the African Bird Club through their Conservation Award program, to the Percy FitzPatrick Institute of African Ornithology, and the University of Cape Town – Travel Grant. This research would not have been possible with their support.

I express sincere gratitude for the competence and efficiency of Dassa Nkini at the Conservation Resource Center – Tanzania who facilitated all official processes necessary for conducting wildlife research in Tanzania. I am also thankful to Aurelia Mtui, Nelson Ole Kwai and Clarance Msafiri for their effort in this regard. I thank the Tanzania Wildlife Research Institute for granting me this opportunity to conduct research and for facilitating access to the study area.

I am grateful to the Brian Harris and Grant Burden through the Grumeti Fund, for enabling my stay in Grumeti and Ikorongo. I am equally appreciative for the support of Michel Allard, Julius Robinson, and Quinton Rochat through the Friedkin Conservation Fund and Tanzania Game Tracker Safaris for hosting me in Mwiba and Maswa. I am especially thankful to Mzee Nessa, my accompanying field assistant, throughout my fieldwork in Maswa.

For collaborative data sharing I owe my appreciation to Sally Archibald, who provided her Africa fire maps which I used in selecting sample sites, and to Grant Hopcraft for providing interpolated maps for estimates of rainfall and nitrogen, and for providing access to the Serengeti-Mara Database. I am also thankful to Howard Fredrick for his teaching assistance in using QGIS.

Finally, I am so grateful to my family, friends and classmates for their support. I am especially grateful to my father, Erwin Kinsey for use of his vehicle for research and for unwavering encouragement. Finally, I express heartfelt thankfulness to me wife, Jana Kinsey who selflessly encouraged me to pursue the masters program, and who remained a source of strength and dedicated encouragement throughout.

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Introduction

Fire in ecosystems

Burning for biodiversity might seem absurd or even contradictory. How can the scorching heat of flames, which causes animals to flee and which burns and withers everything else within its reach, promote life? The paradox that fire is beneficial and indeed essential in some ecosystems is increasingly being supported and acknowledged in the scientific community (Martin & Sapsis 1992, Bond & Archibald 2004, Parr & Andersen 2006). In the absence of fire, some ecosystems would be transformed to alternate states (Bond et al 2005, Staver et al 2011) and key habitats and the species they support would be lost.

Fire is globally pervasive and a major contributor to ecological processes. Its global annual extent is on the order of three to four million km^2 (Dwyer et al 2000, Roy et al 2008), and a major proportion of the Earth's land surface can be classified in pyromes, where fire is a consistently recurring process (Archibald et al 2013). In some systems, such as rain forests and temperate forest its effect can cause immense destruction (Romme 1982, Laurance 2003). But in many systems such as savannas, boreal forest, Mediterranean Chaparral, Californian shrublands and South African Fynbos, its timely recurrence is essential to the creation of habitats and the maintenance of ecosystem processes (Johnson 1992, Bond 1997, Pausas & Vallejo 1999, Keeley & Fotheringham 2001).

Savannas are among the most fire dependent and geographically extensive of these fire driven systems. Their vast expanse through much of sub-Saharan Africa, South America, India and Australia can be attributed in large part to fire (Archibold 1995, Staver et al 2011). These savanna systems support significant human populations and

livestock grazing systems, contributing substantially to pastoralist livelihoods (Asner et al 2004). Savanna systems, particularly in Africa's great safari parks and conservation areas, support important tourism industries which contribute to regional economic growth and development (Fayissa et al 2008). Of course, this tourism industry is dependent on the iconic wildlife found in savanna systems. These include some of the last remaining great large mammal populations such as migrating herbivores and carnivores of the Serengeti in East Africa (Sinclair & Arcese 1995). But beyond the iconic large herbivores and carnivores the savanna biome supports unique biodiversity in birdlife and other less charismatic taxa. Their conservation importance for bird migrations, endemic and range-restricted species warrants targeted research to ensure appropriate management interventions.

A key question in conservation and ecology of fire driven system relates to the source of ignition. Clearly, fire dependency and adaptation develops on evolutionary time scales, so what role do humans have, given our relatively recent presence as ecological engineers? Lightning-caused ignition has been an important part of fire ecology throughout the Earth's evolutionary history, with evidence of natural fire as early as 400 million years ago (Scott 2000, 2010). In contrast Hominids are a more recent force in fire ecology with the earliest active use and control of fire dating to about 1 million years ago (Bird & Cali 1998), with some earlier controversial claims (James et al 1989), and more recent evidence from 790,000 years ago (Goren-Inbar et al 2004).

Ever since *Homo sapiens* and some of our ancestors mastered the use of fire, we have undoubtedly been a major force in fire prone systems (Pyne 2001). Most recently, in the Anthropocene, modern humans have changed background levels of natural fire

activity by precipitating mega-herbivore extinctions, intensifying livestock grazing, clearing forests and fragmenting flammable environments, changing ignition patterns and actively suppressing fires, contributing to substantial ecosystem changes (Aldersley et al 2011, Bowman et al 2011). Human use of fire increase progressively from the late Pleistocene, through the Holocene, and into the Anthropocene with our cultural transition from hunter-gatherer to pastoral, agrarian and industrial societies—with ever growing populations (Pyne 2001). The human dimension started much earlier in Africa than any other continent, allowing fire-controlling humans to evolve in parallel with savannas (Archibald et al 2012). We must acknowledge that we are and have been an integral part of the savanna history. While we do not know exactly how human-ignited fire regimes differ from pre-historical, lightning-driven regimes (Frost 1999), we have a responsibility to be purposeful in our fire management decisions if we intend to maintain the ecological integrity of the savanna.

Despite the role we have to play in savanna conservation, little is known about the effect of fire and different management practices on biodiversity (Parr & Andersen 2006). Fire is already a major conservation management tool and is among the most readily employed active measures in manipulation of open range savanna systems (Van Wilgen et al 1990). However, appropriate fire management interventions have been hampered by cultural aversions to fire or conversely to over-zealous pyromania, to non-adaptive policy, and to our limited understanding of the role of fire in the savanna (Scholes & Walker 1993, Pyne 1997). Despite a major international interest in biodiversity conservation, studies on the effects of fire on fauna in fire-driven biomes are still patchy (Parr & Chown 2003). While it is generally accepted that fire and savanna are

linked, the most effective fire regime for biodiversity management remains unclear, especially beyond the effects for grazers and browsers. This study addresses some of the questions surrounding the effect of recent fire history on birds through its impact on savanna vegetation.

Impacts of fire on savanna

Not all fires are the same. Fires as ecological events occur within a historical pattern of fire attributes known as a 'fire regime'. The nature of the regime determines the way in which fire influences the ecosystem. In particular, fire frequency, seasonality, intensity, and spatial scale interact to influence patterns of savanna vegetation structure (Smit et al 2010).

Satellite data enable us to document recent historical fire regimes. A monthly summarized burned area product from 2000 to present is available from Moderate Resolution Imaging Spectroradiometer (MODIS) through the Land Processes Distributed Active Archive Center (LP-DAAC) (Roy et al 2002, 2005, 2008). On a broad scale, these data have provided a spatially explicit and comprehensive view of fire across the globe revealing the spatial co-occurrence of fire and savanna, especially in Africa, 'The Fire Continent' (Archibald et al 2010). On a finer scale, the satellite data provide a unique opportunity to reveal the underlying ecological processes that are affected by fire and that affect the influence and occurrence of fire.

The effects of fire in savanna can be separated according to temporal effects (Woinarski & Recher 1997). The first immediate effect involves a direct, often destructive impact. This includes the consumption of grassy and understory vegetation, the transformation of dense habitats to open habitats, as well as the direct incineration of

nests, seeds, and immobile invertebrates. In frequently burned systems this immediate impact, which can appear starkly damaging is followed by short-term post fire regenerative period. Finally the influence of recurrent fire disturbances defines the long-term impact involving successional processes and defines the more persistent character of the habitat. These temporal effects are ecologically important but are influenced by other processes (Scott et al 2013).

Fire does not act alone. Its ecological impact, through its influence on vegetation distribution and structure, is mediated by other underlying drivers (Bowman et al 2009). Multiple biophysical processes contribute to determining the occurrence, character and structure of the savanna systems (Walker 1987). In particular savanna structure varies with mean annual rainfall and rainfall seasonality as well as nutrient availability, herbivory and fire (Sankaran et al 2005).

In general, fire tends to promote grasslands at the expense of woodlands but its influence is rarely straightforward and is dependent on the properties of the fire regime and its interaction with these other biophysical processes. Fire and herbivory consume vegetation at different spatial scales and at different structural levels (Levick et al 2009), while nutrients and rainfall determine the available consumable biomass (Bond 2008). Rainfall and rain seasonality mediate the occurrence of fire (Archibald et al 2009). High rainfall areas tend to produce higher biomass and seasonality in rain allows the biomass to become available as fuel for fire. Therefore, while fire is considered an ecosystem driver, the nature of fire regimes and their consequent impact are dependent on multiple other factors.

For wildlife conservation, vegetation structure is important (Tews et al 2004). For herbivores, and consequently their predators, risk of predation determined by vegetation structure is a key predictor of distribution in the savanna (Hopcraft et al 2010, 2012). For birds the link is arguably even more pronounced. Complexity in vegetation structure is a major influence in habitat selection among birds (MacArthur & MacArthur 1961, Willson 1974, Cody 1981). Fire, as a major determinant of vegetation structure in savannas is by extension a major indirect contributor to bird community composition, while also having direct impacts on life cycles.

Much of the limited scientific literature on the impacts of fire and birds comes from the Australian context (Woinarski & Recher 1997). For example, Baker et al (1997) studied the impact of a major fire disturbance in sclerophyll forest in Canberra, Australia and revealed severe and long-term demographic impacts on populations of several bird species. This long-term study looked at demographic effects on the populations but did not take into account the structural changes in vegetation. A similar study by Lyon (1997) also revealed a 60% reduction in total abundance of birds following a major fire in rainforest, heath and eucalyptus in eastern Victoria, Australia. There was significant variation in the impact and recovery of bird populations depending on habitat type. Main losses were among highly mobile species, and remaining species were limited by resource availability rather than their capacity to have survived the fire front. While these Australian studies offer important insight into the impact of fire on birds they are not directly comparable with the African savanna context. The fire events in these examples and often others represent one-time catastrophic high-intensity crown fires in areas unburnt for decades and habitats not adapted to more frequent fire.

African examples have highlighted the important impact of fire vegetation structure in predicting bird community structure. Chalmandrier et al (2013) confirm post-fire successional changes in Cape Fynbos both in vegetation structure and plant functional composition to which bird communities respond. But again, fire regimes in Fynbos are very different than in savannas. Surface grass-fuelled savanna fires have much more rapid post-burn recovery so the immediate impacts are much more ephemeral and their cumulative effects on vegetation structure can be more subtle. However, many savanna specific studies, mostly from South African mesic savannas make only inferential reference to fire, acknowledging the impact of fire on vegetation, but focusing on the link between vegetation structure and composition on bird communities (e.g. Skowno & Bond 2003, Sirami et al 2009, Sirami & Monadjem 2012). There is therefore a need for analysis of the effect of recent and recurrent fires on vegetation and their direct and indirect links to bird communities in the African savanna.

Aiming for heterogeneous mosaics of habitat through variation in fire and grazing patterns is often proposed as beneficial for biodiversity (Brockett et al 2001). While this is an attractive hypothesis, especially with regard to structure-dependent bird assemblages, it has been questioned as an overarching rule (Parr & Andersen 2006), and is not always empirically support (Davies et al 2012). In an experimental study by Fuhlendorf et al (2006) on birds in the American grassland prairies, experimental variation in grazing and burning (including exclusion of both) was confirmed to be beneficial for biodiversity across a mosaic of patches, especially for some specialist species. They concluded that heterogeneity in burning and grazing was advisable as a management strategy. In contrast, a study by Jansen et al (1999) along a land-use gradient

in the South African highland grasslands found that overall bird diversity was negatively associated with even moderate burning and grazing, and burning and grazing differentially affected specific species densities. This study only looked at the effects of burning and grazing on bird density and diversity without considering the link with vegetation structure.

The composition of savanna bird assemblages is often more highly responsive to vegetation structure rather than vegetation species composition (Sirami et al 2009). Savannas are defined by two major structural components. They are characterized by the co-occurrence of a continuous grass layer and a discontinuous tree and shrub layer in the form of open canopy woodlands and bushlands (Scholes 1997). These two structural components are influenced differentially by the immediate and long-term temporal effects of fire.

Firstly, the grassy layer is affected by the immediate fire effect. The direct removal of the grassy and low-level layer results in a transformation of a dense low level vegetation structure to open, sparse structure. Post-fire regeneration of this grassy layer follows, influenced by timing of rainfall, density of herbivores, and availability of soil nutrients (Anderson et al 2007a, Holdo et al 2007). The long-term temporal effect influences the tree and shrub layer. Over 10-15 years, reoccurrence of fires or lack of fire influences mortality and recruitment of trees and shrubs and accumulation of woody biomass. This component is also influenced by the intensity of grazing and browsing, the availability of nutrients, and the patterns of rainfall (Holdo et al 2009a).

The influence of fire on vegetation can be vastly different when considering a range in temporal scales, in light of different regimes, and in relation to the other

biophysical processes. In grasslands the immediate impact of fire and the subsequent regeneration of grasses have important implications on low-level vegetation structure and bird community structure. Over years these successional changes can lead to significant changes in bird species composition (Sirami & Monadjem 2012).

Serengeti ecosystem context

The Serengeti ecosystem provides a complex 'natural laboratory' for investigating the impact of fire (Sinclair & Arcese 1995). A substantial proportion of the ecosystem is burned each year (see Appendix 1 Map 3) making fire an integral part of the system (Sinclair et al 2009). But fire is one explanatory variable in a complex dynamic savanna system with highly interactive interconnected trophic and geophysical components (McNaughton 1992).

The rainfall in the Serengeti is bimodal and highly seasonal with dry periods between the short rains concentrated in November and December, and the long and heavier rains in March through May (Norton-Griffiths et al 1975). This rainfall pattern is a significant determinant of fire seasonality, which is very different than the South African context, from where much of fire research is focused. The mean annual rainfall is distributed across a broad rainfall gradient from ~150mm in the southeast to ~1400mm in the northwest (Norton-Griffiths et al 1975). soil N-value of 0.17%

The nutritional gradient broadly opposes the rainfall pattern with moist dystrophic conditions in the northwest and drier eutrophic conditions in the southeast (Holdo et al 2009a), Ruess and McNaughton (1987) reporting a soil nitrogen range of 0.14 – 0.39% from several across the Serengeti. These underlying geophysical drivers contribute substantially to the character of the savanna from drier nutrient rich short grass plains in

the southern *Acacia – Commiphora* woodlands to wetter, nutrient poor tall *Themeda* grasslands in the northern *Terminalia – Combretum* woodlands (Sinclair & Arcese 1995)

Bottom-up drivers, namely nutrient availability and rainfall, mediate the effect of the two major top-down drivers, herbivores and fire in the Serengeti savannas (McNaughton 1985). Serengeti has impressively high populations of mega-herbivore grazers including around 1.3 million migrating wildebeest, 200,000 zebra, 440,000 Thomson gazelle, 70,000 buffalo, as well as eland, Grant's gazelle, topi and others (Mduma et al 1999, Holdo et al 2007, Sinclair et al 2009). Browsers also play a significant role as top-down drivers with the most significant influence being exerted by the elephant population (Dublin et al 1990, Sinclair et al 2009). These populations compete with fire for consumable biomass and therefore their density is important in mediating the occurrence of fire.

The biotic top-down drivers have been subject to major human perturbations that have had knock on effects for fire. The introduction of rinderpest virus in the late 19th century led to a catastrophic die off of wildebeest and buffalo, whose populations were reduced to by as much as 95% (McNaughton 1992). The successful disease eradication in 1963 permitted an impressive recovery of these populations.

Similarly, elephant numbers have fluctuated in the last century due to the ivory trade and poaching. They were present in the ecosystem in the 19th century (Fosbrooke 1968) but disappeared from the Serengeti until recolonizing in 1955 (Lamprey et al 1967). Poaching in the 1970s reduced their numbers again from 3500 to 400 animals (McNaughton 1992). The population has since recovered but a new wave of poaching

across Africa once again raises questions about the fate of elephant in the Serengeti (Wasser et al 2009).

Fire in the Serengeti is almost exclusively set by humans, with no known incidence of lightening ignition (Sinclair & Arcese 1995). However, despite the management influence, the distinct spatial and temporal pattern of fire is largely determined by the flammability of the landscape in response to rainfall, nitrogen, and herbivore density. Fire responds to the bimodal rainfall seasonality by exhibiting fire seasons with different characteristics. Early burning (May-July) after the heavy rains tends to be characterized by cooler patchier fire through still-moist vegetation. Late season burns (August-October) before the short rains tend to be hotter and their patchiness is determined more by the presence of consumable biomass rather than vegetation moisture. November – January marks a period of minimal fires followed by a short burn season (February – April) in the high rainfall region. The opposing rainfall and nitrogen gradient result in taller grasses and more flammable biomass in the west and particularly in the northwest where fire return intervals are shorter and short season burns are possible (Sinclair et al 2009).

As a major consumer of grassland vegetation, less discriminating than feeding herbivores, fire competes with and supplements the top-down process controlling savanna structure (Bond & Keeley 2005). Historically, in response to the fluctuating herbivore numbers and the consequent fuel load, fire occurrence and influence changed. Crucially, the recovery of wildebeest was strongly correlated with reduced fire prevalence in northern woodlands (Sinclair et al 2009).

Historical changes in woodland-grassland dynamics in the Serengeti-Mara ecosystem have been attributed in large part to changes in fire regimes in association with major herbivores (Dublin et al 1990). These interactions between fire, and herbivory mediated respectively by management decisions, disease and poaching, play critical roles in determining different habitat types and structures in association with rainfall, nutrients (Holdo et al 2009a, Reed et al 2009). More recent remote sensing data in the Serengeti ecosystem reveal a significant influence of fire seasonality in determining woody cover in woodland savanna and fire intensity explaining patterns in grassland savanna areas (Dempewolf et al 2007).

In conservation areas, fire management policies and the capacity to implement them have important ecological implications (Van Wilgen et al 2004). The use of fire as a management tool is widespread in Tanzania and is one of very few active protected area management interventions. Historically, managers have adopted a blanket approach; using the same fire regime across wide areas to achieve a relatively limited set of objectives. For the Serengeti, up until the 1970s, this meant a maximal burn strategy in the late season (Sinclair et al 2009). This was a practice carried over from the pre-national park pastoralist system to promote grass growth for grazers at the onset of the rainy season. With a sharp decline in wildebeest and buffalo in the late 19th century, this strategy resulted in increased hot burns that limited tree recruitment and eventually led to rapid decline in woodland cover from between the mid-1940s to 1980, due to lack of new recruitment and assisted by a recovering elephant population (Sinclair et al 2009).

Since the 1970s, in response to the loss of woodlands there was a one-time shift in fire policy away from late season burning to maximal early season burning in an effort to

encourage recruitment of woody vegetation (Sinclair et al 2009). This strategy has remained the status quo until more recent discussion on revisiting the burning policy and shifting toward more adaptive approaches. Managers in the reserves outside the national park have already adopted more ecologically guided, adaptive strategies and in the Serengeti there is progress towards implementation of a recently adopted Serengeti Fire Management Plan (TANAPA Ecological Monitoring Department 2013).

While there is new momentum with regard to fire decision-making, the focus remains on migrating herbivores and little attention has been given to addressing other conservation objectives. The Serengeti is a large 'Important Bird Area', and an 'Endemic Bird Area' home to several avian endemics and range-restricted species (Baker & Baker 2001). The species of particular conservation interest include Grey-breasted Spurfowl (*Pternistis rufopictus*), Fischer's Lovebird (*Agapornis fischeri*), Usambiro Barbet (*Trachyphonus darnaudii usambiro*), Rufous-tailed Weaver (*Histurgops ruficauda*), Karamoja Apalis (*Apalis karamojae*), and Grey-crested Helmet-shrike (*Prionops poliolophus*).

While these species are not yet listed as threatened by the International Union for Conservation of Nature (IUCN) Red List (http://www.iucnredlist.org), all but the Usambiro Barbet and Rufous-tailed Weaver have declining population trends (IUCN 2013). Their long-term conservation status and ecology is most probably linked to regular fire disturbance. Burning in different seasons may affect different species in different ways. The Grey-breasted Spurfowl for example is a ground nesting species in savanna woodland. Early burning, which has been the default strategy, coincides with their nesting period and presumably has a direct effect on nesting success. Another example is

the Grey-crested helmet shrike whose numbers appear to have increased in the Grumeti reserve since fire management strategies shifted away from early season burns. Investigating these effects and drawing more general conclusions will allow managers to be better informed about impact of the decisions they make.

Since fire is the only deliberately manipulated driver of the Serengeti ecosystem knowing how ecosystems respond to fire regimes is vital for ecologically appropriate management. Understanding the mechanistic response of species, spatial and temporal effects of fire, and interactions with other processes is critical for achieving conservation goals (Driscoll et al 2010). Long-term research addressing management questions is necessary to develop ecologically sustainable fire management practices for biodiversity conservation. Historical remote sensing data series and observations of current patterns can contribute to understanding the role of fire in savannah ecology.

Aims and hypotheses

There is little information on the influence of regular occurrence and timing of fires on bird composition, density, and diversity in the African savanna. In other habitats, research indicates that fire has a direct impact on birds (Woinarski & Recher 1997; Fuhlendorf et al 2006), but in the African savanna context where fire is frequent the effects are less apparent (Mills 2004) and many questions remain largely untested. Research also suggests the strong impact of fire on vegetation structure, which has been the primary focus of fire science (Pyne 1997). The link between vegetation structure and bird communities has also been investigated in African savanna (Skowno & Bond 2003; Krook et al 2007, Sirami et al 2009, 2012). A question that has yet to be fully explored is the link between fire and vegetation, vegetation and birds, and thus indirectly, the impact

of fire on birds through its impact on vegetation. This question, addressing the influence fire history on birds, was the primary focus of investigation. Specifically, this study focused on the effects of fire on birds, fire on vegetation structure, and to corroborate the link, the effect of vegetation structure on birds, to which they are known to be sensitive.

The logical sequence of investigation followed analyses of the following effects:

a. Birds as explained directly by fire history parameters to establish the association;
b. Vegetation structure as explained by fire history parameters to investigate a plausible mechanism; and
c. Birds as explained by vegetation structure to corroborate research on habitat sensitivity.

The effects of fire were divided into recent event effects and historical regime effects. Specifically, the variable of interest for recent fire history was the occurrence or nonoccurrence of a fire event in the last calendar year (last fire). The variables of interest for fire regime effect were summarized as cumulative recurrences and seasonal timing of fires since 2000, in each of three fire seasons: early (May-July), late (August-October) and short (February-April). We expected birds to respond differentially to the fire history patterns and we hypothesized that vegetation structure would be associated with the occurrence of the last fire event, and the cumulative number of fires in each season.

A series of raw vegetation structure measures were summarized in two principle components, characterizing the grassy understory and the mid-upper level canopy. We expected birds to respond differently to changes in these structural layers. We also

hypothesized that recent fire events and cumulative regime history would affect these structural layers differentially.

These effects of fire and vegetation on birds were tested for several bird parameters including community composition, diversity and abundance. We hypothesized that each of these parameters would be influenced by recent fire event history (<12 months) and cumulative fire regime history (since 2000) and that vegetation structure would show effects in these parameters.

For the effect of fire on birds, our first hypothesis tested whether a recent fire event, within one calendar year, impacted the structure of the bird community. Secondly, we test whether bird community composition was significantly correlated with cumulative fires since 2000, in each of three fire seasons: early (May-July), late (August-October) and short (February-April). Finally, we test the hypothesis that recent fire events negatively impact overall abundance and diversity of birds, and that a regime of high recurrence of fire would also impact bird diversity and abundance.

The subsequent analyses of the effect of fire on vegetation investigated a possible mechanistic explanation for the influence of fire history patterns on birds. The expectation follows that fires influence vegetation structure, and consequently birds respond to vegetation structure. In order to get at this indirect impact of fire on birds, it was necessary to investigate the direct impact of fire on vegetation and thereafter the consequent response of birds to vegetation. For the purposes of this study we separate the effect of fire on vegetation into two temporal effects. The first included the immediate effect of a fire event and the post-burn recovery period, which we expected to be detectable in recently burnt areas, in contrast to areas unburnt for over one calendar year.

The second concerned a longer-term regime impact primarily influenced by the reoccurrence of fire across different fire seasons. We derived a measure of this from cumulative fire history – cumulative burns over 14 years in each of three fire seasons defined earlier: early, late and short. We expected these two temporal effects to act differentially on the two major structural components that make up the savanna: the low grassy understory affected largely by occurrence of a recent fire event and the mid-upper shrub/tree layer affected by cumulative fire regime history.

Specifically, we predicted recent fire history to have a negative effect on vegetation density of the lowest savanna structural component, made up of the grassy understory. Each year in which a fire occurs this grassy understory is removed changing the near-ground structure. We tested the hypothesis that a recent fire event would result in open low-level structure, while recent fire non-occurrence would result in denser understory.

Similarly, we predicted the long-term effect of cumulative fire regime derived from recurrence of fire over the course of 14 years to influence the woody plant structural component. We expected the impact of accumulated burns since 2000 in each fire season to influence growth and recruitment of woody vegetation that makes up this structural component. We predicted that for any given rainfall and nutrient regime, more fires in general would open mid-upper level structure while no fires would result in denser mid-upper level structure. More specifically, we expected this effect to be strongest for late season fires that are hottest as opposed to cooler, patchier early burns.

Finally, we tested the relationship between birds and vegetation structure to complete the causal link of fire on vegetation, and vegetation on birds. Different bird

assemblages are expected to occur along this gradient from open to dense low-level understory. We tested the hypothesis that bird community composition changes according to density of this understory to complete the link between recent fire event history and bird species composition. We tested a final hypothesis that greater structural density in both understory and shrub-tree layers would yield higher density and diversity of birds, as foliage density can be associated with greater structural complexity (Tews et al 2004). We postulated that greater vertical structure in vegetation would offer greater habitat structure for bird species to exploit.

Methods

To investigate the short-term and long-term impacts of fire on birds, we tested the direct ordination structuring effects and regression trends of recent fire event occurrence and cumulative fire regimes on bird community composition, diversity, and density. We expected fire to influence birds though its impact on habitat alteration, so we tested the structuring effects and regression trends of fire variables on vegetation structure. Finally we tested the effect of vegetation structure on bird communities. Each of these analyses involved incorporating the impacts of rainfall and nitrogen as underlying drivers. To carry out these tests, we determined the underlying physical environmental context by mapping fire activity from remote sensing data in conjunction with interpolated maps of rainfall and nitrogen gradients. Collecting bird community and vegetation structure data in the field involved a suite of sampling techniques at sites distributed to cover the full range of environmental variability.

Study area

The study area included much of the greater Serengeti ecosystem in Tanzania between 2° and 3.6° South and 33.9° and 34.9° East. It comprised parts of western Serengeti National Park, Maswa Game Reserve, Makao Conservation Area, Grumeti and Ikorongo Game Reserves (Appendix 1 Map 1). This area includes a near complete range of Serengeti ecosystem habitats across a broad rainfall gradient, from dry eutrophic *Acacia* - *Commiphora* woodland and short grass plains in Makao Conservation Area, to the moist dystrophic *Terminalia* - *Combretum* woodlands and tall *Themida* grasslands in the Ikorongo and Grumeti Game Reserves. Fire is a major contributor to the ecology of this area with over 80% of the protected land area in the National Park and western protected areas experiencing a fire at least once since 2000 (at 500-meter resolution) (Appendix 1 Map 2d).

Data collection

Fire data

We obtained the complete times series of MCD45A1 Moderate Resolution Imaging Spectroradiometer (MODIS) Burned Area product for the study area through the Land Processes Distributed Active Archive Center (LP-DAAC) using the EOS Data Gateway web interface located at http://reverb.echo.nasa.gov. This product algorithm identifies and directly maps the spatial extent of the area affected by fire at 500-meter resolution and summarizes the data on a monthly basis (Roy et al 2002, 2005, 2008). The complete time series covered January 2000 through October 2013. We extracted a number of burn metrics from these data. This involved mapping the total number of fires across the time series (Appendix 1 Map 2d) and subsetting the data across four annual quarters each representing one 'fire season'. To summarize cumulative fire occurrence

for each of these fire seasons, we divided the seasons as such: early burn season in May-July (Julian days 121-212) (Appendix 1 Map 2a), late burn season in August-October (Julian days 213-304) (Appendix 1 Map 2b), minimum burn rainy season in November-January (Julian days 305-366, 1-31) (unmapped), and short burn season in February-April (Julian days 32-120) (Appendix 1 Map 2c). Finally, we determined the number of seasons since the last fire occurrence ('last burn') to identify occurrence/non-occurrence of fire within one calendar year (Appendix 1 Map 3). We used invalid MODIS data pixels, with insufficient data to be classified as burned or unburned, to cross-check that the points selected for fieldwork had no more than 5% invalidity across all months. This rate was sufficient given that invalidity occurs mainly due to extended cloud cover mainly during months of minimal fire occurrence.

Rainfall data

Serengeti Ecology Department collected monthly rainfall records from 58 rain gauges. Using these long-term (1960–2006) data, Hopcraft et al (2012) created a smoothed rainfall map by regression kriging across a known southeast to northwest rainfall gradient. We extracted interpolated mean annual rainfall values from the map for each sample site.

Nitrogen data

Using grass nitrogen estimates as a proxy of fertility, we extracted estimates for each sample site from a grass nitrogen map provided and described by Hopcraft et al (2012). They took samples of wet season grass at 148 sites across the ecosystem and measured nitrogen concentrations of dried grass samples using a near infra-red spectrophotometer. They produced a spatial distribution map of grass nitrogen from

interpolation by regression kriging using a 9-year mean Normalized Difference Vegetation Index (NDVI) as a covariate.

Fieldwork

Sample selection

We selected sampling points from MODIS MCD45A1 product 500m burn pixels centroids using fire maps provided by Archibald et al (2010). The sample was randomly selected, stratified by number of burns since 2000 to ensure broad coverage across sites with different burn regimes. We limited our sample to within 250 meters of roads to facilitate accessibility. We selected points across the Serengeti Ecosystem rainfall gradient from just north of the L. Eyasi escarpment in Makao Conservation Area in the southeast to Grumeti and Ikorongo Game Reserves in the northwest. At each point we used a suite of rapid sampling techniques to characterize bird communities and vegetation structure. We sampled 207 sites once each during late September to early December 2013—at the end of the long dry season and beginning of the short rainy season (Appendix 1 Map 1). We used this one-stop sampling approach to enable sampling a high number of sites and broad geographic coverage across the range of environmental variability. The trade-off of this one-stop approach was an expectedly high degree of variance in bird community and vegetation structure measures. However, we expected effect sizes to be strong enough to be detectable despite this high degree of variance in the dataset.

Bird community sampling

We conducted standard 10-minute point counts (Bibby 2000) in the morning between 06:30 and 11:00 during peak bird activity for highest detection rates. During the 10-minute point counts, we recorded bird species, abundance count, and distance from

observer for each visual or audible detection within distance bands of radius 0-10 m, 10-25 m, 25-50 m, 50-100 m, >100 m, and fly-overs. We included raptors and aerial feeders (e.g. swallows, swifts and bee-eaters) as fly-overs or included them in the distance band of initial detection if we judged them to be actively feeding within the habitat as opposed to simply transiting through. We also made records for unidentified audible or visual detections.

Vegetation sampling

We conducted the Bitterlich variable-plot point sampling method (Cooper 1957) to provide a measure of tree density around each sample point. We used a wedge angle gauge: held at a fixed distance from the observers eye and rotated 360° around the sample point to obtain a count of trees and bushes whose trunk or stem diameter was visually wider than the wedge, which represents a fixed angle. Closer trees, and larger trees are counted proportionally more often. We then multiplied this count by a basal area factor according to the wedge size to give the total stand basal area (SBA) at breast height in m^2 per hectare at each sample point.

We measured horizontal visual obstruction caused by vegetation to characterize habitat structure using methods devised by MacArthur & MacArthur (1961), and modified from Ralph (1985), and Skowno & Bond (2003). We generated foliage profiles at each sample point using this simple method by estimating distance of horizontal visual obstruction at specific heights in a single direction. The distance we recorded at each height was an estimate of the distance at which an imagined 10x10cm board would be >50% visibly obscured by vegetation. The specific heights were 0.05, 0.25, 0.5, 1, 1.5, and 2 meters from the ground. We capped distances estimates at 250m. At each sample

point, we took a foliage profile firstly in a random direction from the sample point. We took three more profiles in new directions, each perpendicular to the previous direction and five paces from the previous point. Additionally, we also estimated maximal canopy height in each direction within 100m.

We used a disc pasture meter (DPM) as a rapid method of measuring compressed grass height to give a proxy for the grass layer's contribution to the vegetation structure (Bransby & Tainton 1977). We took ten DPM readings at 5-meter intervals in a random direction from the sample point, and focused analysis on the mean of these values. This provided a measure for a major component of the savanna habitat that is directly impacted by fire, herbivory, and abiotic conditions.

Data preparation

We used R 3.0.1 (R Development Core Team, 2013) to perform data manipulation and analyses through the integrated development environment RStudio (RStudio, 2013). We converted raw bird abundances from point counts to density estimates for each species at each point. We did this to take into account that species differ in their individual detectability, and detectability decreases with distance from the observer. We fitted raw bird point count data to detection functions for each species to characterize the decay of detectability with distance from the sample points using package mrds (Laake et al 2013). We used this detection probability function to multiply raw abundance in each distance band by its distance-specific detection probability to obtain a single density estimate for each species at each point. For less common species, however, records were often too few to accurately fit a detection function, in which case we pooled data among similar species until samples size was sufficient. We set an a priori threshold of >45 detections in

separate distance bands for fitting an individual species detection function. We grouped other species below this threshold according to five exclusive species categories; large, medium, small and aerial and grass dwelling (Appendix 2 Table 2). We used species densities to construct a community matrix of density/absence of each species for each sample point. We also took a subset of common species (contributing >1% to the total bird density at all sites) to repeat the analyses to reduce the effect of very rare species found only at one or very few sites.

Data preparation for multiple regression analysis of bird data required deriving single parameters for each point from the point count distance-sampling data. We calculated avian species total density, and Shannon diversity index (H) for each sample point. [$H = -\Sigma\ p_i\ (\log\ p_i)$ where p_i is the proportional abundance for each species at a sample point (Shannon & Weaver 1949)].

We aggregated the repeated vegetation structural measures for each point sample to obtain a central tendency value for each measure. We took the inverse of all visual obstruction distance as a measure of foliage density (thereby high/low values indicating dense/sparse vegetation respectively). The resulting data frame consisted of inverse median visual obstruction distances at each height (0.05m, 0.25m, 0.5m, 1.0m, 1.5m, 2.0m), median maximal canopy height ($canopy_{max}$), mean DPM reading (DPM_{grass}) and estimated stand basal area (SBA) at each sample point.

Subsequently, we summarized vegetation structure in two principal components using the package vegan (Oksanen et al 2013). We used the natural $\log_e$ of all vegetation measures to de-emphasize high values. The first two axes of this PCA accounted for >75% of the variation in the data. The first axis, which explained 53% of the variance,

described a vegetation structural gradient from sample points dominated by closed dense foliage (low PC1 value) to open sparse foliage (high PC1 value). Lowest level vegetation explained least variation on this axis.

The second axis, which explains 22% of the variance, distinguished points which were dominated by tall grasses and dense low level vegetation (low PC2 value) from those which were clear, open low-level vegetation (high PC2 value). Mid-upper vegetation measures (1.0m – $canopy_{max}$) described some of this variation being inversely correlated with lower level structure (DPM_{grass} – 0.5m). Eigenvectors and plots for the first two axes of a Principle Component Analysis explaining 75% of the variance in vegetation structural measures are provided in Appendix 2 Table 1, Appendix 2 Figure 1. Subsequently, we used these first two principle components as independent variables characterizing the two major vegetation structural components – lower grassy layer and mid-upper shrub/tree layer.

Analyses

We divided analyses into two parts; the first relating to the composition, diversity, and abundance of birds as explained by fire, and the second concerning the indirect influence of fire on birds through its effect on habitat structure.

We used multivariate analyses to test the first hypotheses relating bird community composition to fire incidence. By conducting constrained correspondence analyses (CCA) using the package vegan (Oksanen et al 2013), we identified the explanatory contribution of recent fire event occurrence within one calendar year as a predictor of bird community composition. We used the same analysis to test whether bird

composition is significantly structured by cumulative fires since 2000 in each of three fire seasons: early (May-July), late (August-October) and short (February-April).

We conducted multiple regression analysis to test the hypothesis that recent fire events, and generally regimes with higher number of fires negatively impact abundance and diversity of birds. We constructed linear models using generalized least squares (GLS) to fit spatially explicit models using the package nlme (Pinheiro et al 2013) to take into account spatial autocorrelations (Beale et al 2010). We constructed GLS, one at a time, for analysis of bird density, and Shannon indices at each sample as explained by fire variables, including underlying nitrogen and rainfall.

We conducted similar multivariate analyses to test the secondary hypotheses that occurrence of a recent fire event and cumulative fire regimes impacted overall vegetation structure. We conducted CCA to identify the explanatory contribution of fire variables as predictors of raw vegetation structure measures. We subsequently included independent and additive explanatory influence of mean rainfall and nitrogen as underlying environmental covariates.

We conducted multiple regression analysis to test the specific differential impact of recent fire events versus cumulative fire regimes on vegetation structure. We constructed GLS models, one at a time, to test the response of the first two principle components describing the vegetation structure (PC1 and PC2) in relation to recent fire events, cumulative fire regimes, nitrogen, and rainfall. In so doing, the models tested the hypotheses that: a.) Occurrence of a recent fire event, within one calendar year would result in open low-level structure (high PC2), while recent fire non-occurrence would result in denser understory (low PC2) and b.) For any given rainfall and nutrient regime,

more fires in general, but especially in the late fire season, would lead to open mid-upper level structure (high PC1), while conversely no fires would result in denser mid-upper level structure (low PC1). Additionally, we conducted bivariate regressions of the influence of rainfall on stand basal area, grass biomass ($DPM_{grass)}$ and cumulative number of burns over the time series, and the influence stand basal area (SBA) on cumulative number of burns. We conducted these analyses to test fire prevalence as a function of rainfall, and its impact on vegetation, and to put Serengeti vegetation density patterns in the context of global trends (Lehmann et al 2014).

After testing the response of vegetation structure to fire, we tested the consequent response of birds to vegetation structure. This involved final analysis of testing bird community composition, diversity and abundance in response to vegetation structure. We conducted CCA to test whether vegetation structure (PC1 and PC2) is a strong predictor of bird community structure. We did this to test specifically whether bird assemblages change along a gradient from open to dense low-level understory (PC2), and mid-upper level shrub/tree layers (PC1).

Finally, we constructed GLS models, one at a time, for analysis of total density, and Shannon Indices of the bird community as explained by vegetation structure (PC1 and PC2). This tested the hypothesis that greater vegetation structural density in both understory and shrub-tree layers would yield higher bird density and diversity.

We tested the significance of CCA constrained axes using an ANOVA-like permutation test to examine the constrained model relative to the unconstrained model. We reported the resulting pseudo-F statistic, which is analogous to the F statistic in ANOVA, p-value, and number of permutation (N.Perm). We conducted bird community

composition analyses for the full bird community matrix as well as a subset of common species to reduce the effect of very rare species found only at one or very few sites.

For each regression analysis, we constructed a full model, including all relevant environmental covariates and their one-way interactions and by stepwise multiple regression by backward elimination using χ^2 tests of the likelihood ratio (LRT) we identified the minimum adequate model that best described the variation in the data (Whittingham et al 2006). Therefore, while we presented hypothesis tests sequentially, in practice, we tested multiple hypotheses simultaneously through the stepwise elimination process.

Results

Sample sites contained a total of 204 bird species excluding unidentified records (Appendix 2 Table 2). The number of bird species on each plot ranged from 8 to 32, with a mean of 18.4. Common species, contributing >1% to total density included 32 species. Bivariate results of the influence of rainfall on tree density (SBA) revealed a significant negative correlation ($\chi^2 = 21$, df = 1, $p < 0.0001$) but we found no significant correlations between rainfall and grass biomass (DPM_{grass}), or the response of total cumulative burns to rainfall and tree density (SBA) (Appendix 3 Figure 1).

Fire effects on bird community structure

The occurrence/non-occurrence of a recent fire event explained a small but significant proportion (0.78%) of the variance in bird community composition (pseudo-$F_{1,205} = 1.6$, $p < 0.005$, N.Perm = 199). Repeated analysis for a subset of common birds yielded slightly stronger structuring (1.5%, pseudo-$F_{1,205} = 3.1$, $p < 0.005$ N.Perm = 199). Cumulative fire in each season also explained a small but significant proportion of the

variance in bird community composition (Table 1).

Table 1 CCA ordination results for analysis of bird species composition constrained by cumulative fire since 2000 for each of three fire seasons: early, late, and short. All variables exhibited significant structuring of bird community composition ($p < 0.005$ N.Perm =199).

Bird community data	Season	Accounted variance	pseudo-$F_{1,205}$
All species	Early	0.74	3.1
All species	Late	0.86	1.8
All species	Short	1.4	2.9
Common species	Early	1.2	2.4
Common species	Late	1.3	2.6
Common species	Short	2.1	4.4

Collectively all fire parameters explained 3.6% of the variance in bird community composition (pseudo-$F_{4,202}$ =1.9, $p < 0.005$, N.Perm = 199) (Figure 1a), and 5.49% of common species community composition (pseudo-$F_{4,202}$ = 2.93 $p < 0.005$ N.Perm 199) (Figure 1b). In comparison, nitrogen and rainfall parameters also explained a small but significant proportion of variance in bird community composition, nitrogen 1.6% (pseudo-$F_{1,205}$ = 3.8, $p < 0.005$, N.Perm 199), and rainfall 1.8% (pseudo-$F_{1,205}$ = 3.8, $p < 0.005$, N.Perm 199) (Appendix 3 Figure 2).

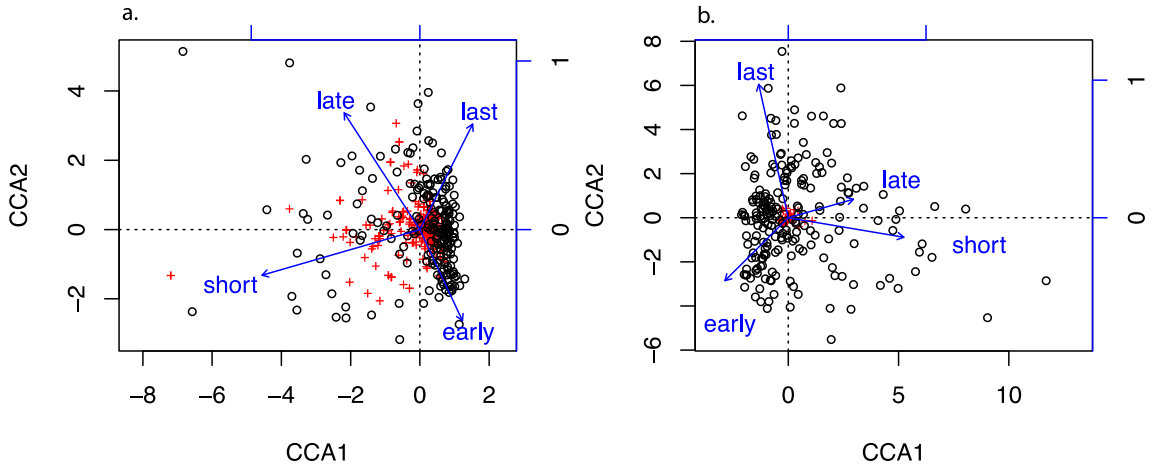

Figure 1 CCA ordinations of bird community structure. Bird species (+) and sample points (o), constrained by all fire variables: cumulative burns in early, late, short fire season, and recent occurrence of the 'last' fire event. **a.** Ordination for all species, **b.** Ordination for common species only.

Fire effects on bird diversity & density

Multiple regression analysis revealed some of the specific effects of fire on bird diversity and density (Appendix 3 Table 1 and 2 respectively). Shannon diversity was significantly correlated with the interaction of nitrogen and occurrence of a recent fire event (Figure 2a). Further investigation revealed a weak negative effect of nitrogen on Shannon diversity when the last fire event occurred recently, and a weak positive effect when the last fire event occurrence was over one year ago ($\chi^2 = 9.6$, df = 1, $p < 0.005$).

The interaction of nitrogen and cumulative burns in the short fire season was also highly significant in determining Shannon diversity (Figure 2b)($\chi^2 = 13.5$, df = 1, $p < 0.0005$). As nitrogen increased the significant positive effect of cumulative short season burns became stronger. Cumulative burns in early and late fire season were not significantly associated with bird Shannon diversity (early: $\chi^2 = 0.039$, df = 1, p = 0.8,

late: $\chi^2 = 1.6$, df = 1, p = 0.2). Rainfall was negatively correlated with Shannon diversity ($\chi^2 = 13.5$, df = 1, $p < 0.0005$) (Figure 2c).

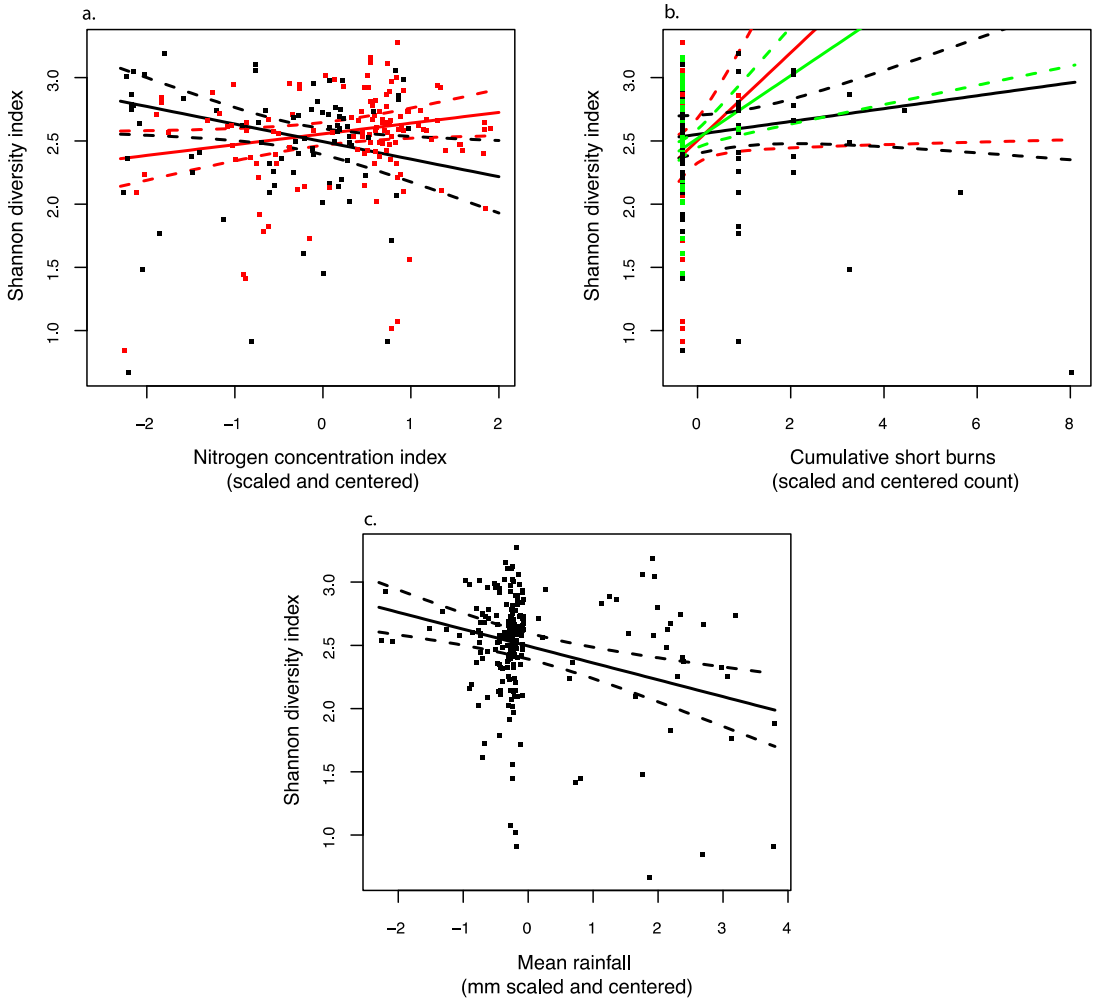

Figure 2 Responses of bird Shannon diversity to covariates derived from the minimum adequate GLS model. Solid and dotted lines represent model predicted values and their respective 95% confidence limits. **a.** Nitrogen in sites without a recent fire event (red) and with a recent fire event (black) in the last calendar year. **b.** Cumulative burns in the short season at low (black), intermediate (green) and high (red) nitrogen values for illustrative purposes representing the bottom, middle and upper third quantiles of the data. **c.** Rainfall.

Total bird density was significantly correlated with the interaction of rainfall and cumulative burns in the short fire season (Figure 3a) ($\chi^2 = 5.2$, df = 1, $p < 0.05$). As rainfall decreased the significant positive effect of short season burns became stronger. Cumulative late season fires showed a weak but significant negative correlation with bird density (Figure 3b)($\chi^2 = 5.2$, df = 1, $p = 0.02$). Cumulative burns in the early fire season and occurrence of a recent fire were not significantly associated with bird density (early: $\chi^2 = 2.8$, df = 1, $p = 0.09$, late: $\chi^2 = 3.4$, df = 1, $p = 0.07$).

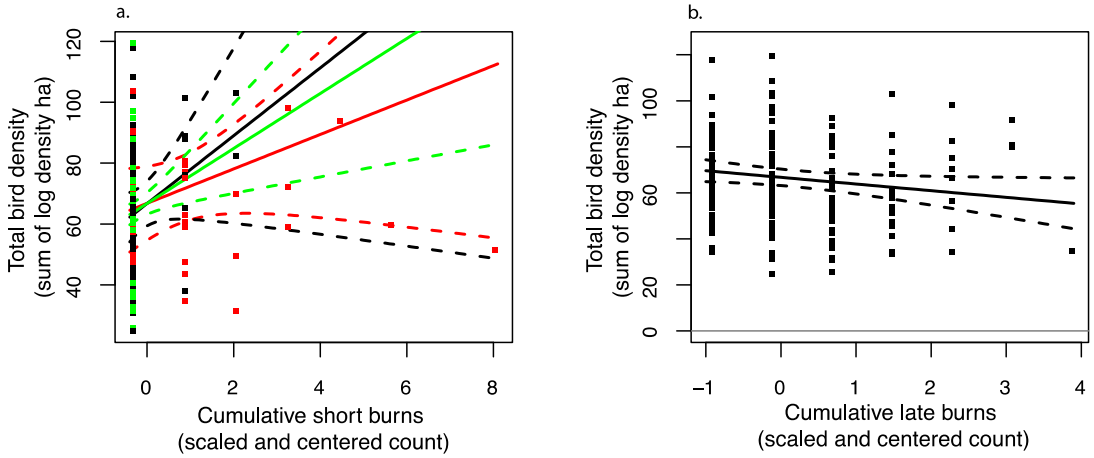

Figure 3 Response of bird density to covariates derived from the minimum adequate GLS model. Solid and dotted lines represent model predicted values and their respective 95% confidence limits. **a.** Cumulative short season burns at low (black), intermediate, (green), and high (red) rainfall for illustrative purposes representing bottom, middle and upper quantiles of the data. **b.** Bird density was significantly negatively correlated with rainfall.

Fire effects on vegetation structure

CCA ordination of raw vegetation structure measures was not significantly structured by cumulative fires in early, late, and short fire seasons collectively (1.4% accounted variance, pseudo-$F_{3,203} = 0.93$, $p = 0.6$ N.Perm = 99) (Figure 4a). We found similar non-significant results for individual cumulative burns (Appendix 3 Table 3). Structuring for raw vegetation measures constrained by cumulative fires in early, late,

and short season with addition of nitrogen and rainfall was also not significant (4% variance accounted pseudo-$F_{5,201} = 1.7$, $p = 0.3$, N.Perm = 99).

In contrast, the occurrence of recent fire event explained a modest but significant 3.7% of the variance in raw vegetation structure measures (pseudo-$F_{1,205} = 7.8$, $p < 0.01$, N.Perm = 199). Combining recent fire event occurrence, nitrogen, and rainfall yielded slightly stronger structuring, with 5.8% of variance accounted (Figure 4b)(pseudo-$F_{3,203} = 4.2$, $p < 0.01$, N.Perm = 299). However, variance in vegetation structure was not significantly explained by nitrogen or rainfall alone (Appendix 3 Table 3). Collectively nitrogen, rainfall, and fire explained a moderate but significant proportion of the variance (8.35% pseudo-$F_{6,200} = 3.04$, $p < 0.01$, N.Perm = 199).

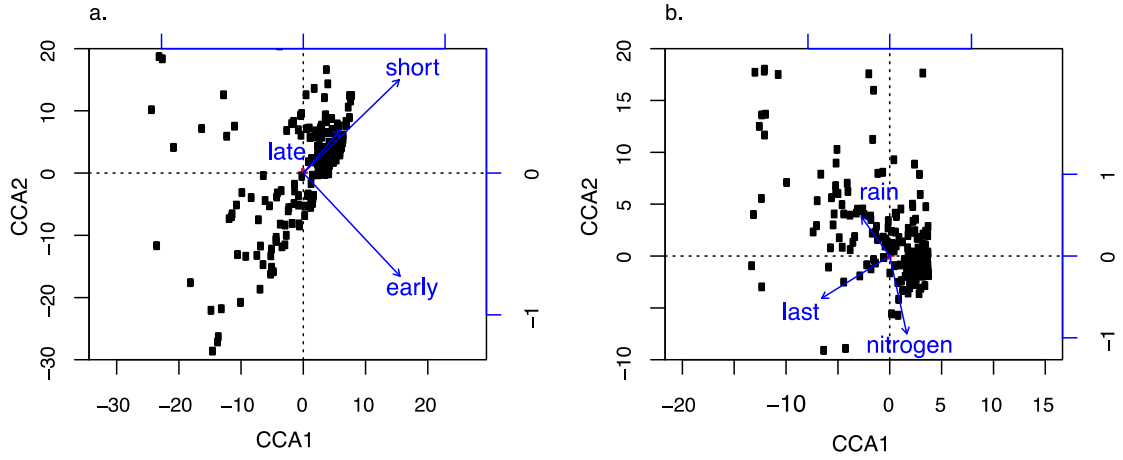

Figure 4 CCA ordination of raw vegetation structure measures for all sample points constrained by **a.** cumulative burns in early, late, and short fire season and **b.** occurrence of a recent 'last' fire event, nitrogen, rainfall.

The results of multiple regression analysis revealed the impact of recent fire events versus cumulative fire regimes on low-level vegetation structure (Appendix 3 Table 4). Vegetation structure PC2, characterizing density of low grassy understory (low/high PC2 value corresponding with dense/open vegetation respectively), was significantly

correlated with the interaction between nitrogen and occurrence of a recent fire event (χ^2 = 8.2, df = 1, p < 0.005). Where a fire event occurred recently within the last calendar year, nitrogen exhibited a weak negative but not significant effect on PC2, and where a fire event had not occurred recently, nitrogen exhibited a weak positive and marginally significant effect on PC2 (Figure 5a). Cumulative burns in early, late and short fire season were not significantly associated with low-level vegetation structure (early: χ^2 = 0.039, df = 1, p = 0.8, late: χ^2 = 0.042, df = 1, p = 0.5, short: χ^2 = 0.0040, df = 1, p = 0.95). PC2 was significantly correlated with the interaction of nitrogen and rainfall (χ^2 = 7.4, df = 1, p = 0.01). As rainfall increased, the effect of nitrogen on PC2 changed from positive to negative (Figure 5b). However, confidence limits suggest that the main effect is not significant.

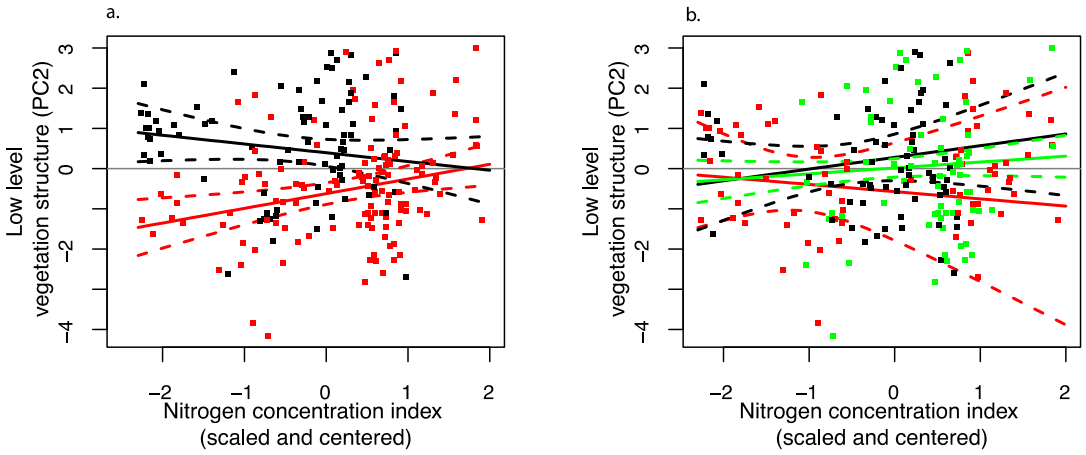

Figure 5 Response of low-level vegetation structure (PC2) to covariates from the minimum adequate GLS model. Solid and dotted lines represent model predicted values and their respective 95% confidence limits. **a.** Nitrogen in sites unburnt for over one calendar year (red) and sites experiencing a recent fire event (black) sites. **b.** Nitrogen at low (black), intermediate, (green), and high (red) rainfall for illustrative purposes representing bottom, middle and upper quantiles of the data.

The influence of fire on mid-upper level vegetation structure (PC1) was generally weak (Appendix 3 Table 5). Vegetation structure PC1, characterizing the mid-upper level vegetation structure (low/high PC1 value corresponding with dense/open vegetation respectively), was significantly correlated with the interaction of cumulative short season fires and the occurrence of a recent fire event ($\chi^2 = 9.9$, df = 1, $p < 0.005$), (Figure 6a) such that the cumulative number of short season fires was positively correlated with open, sparse mid-upper level vegetation in recently unburnt areas, but the effect was weaker in sites experiencing a recent fire event.

Cumulative late season fires also exhibited a marginally significant positive correlation with open vegetation structure ($\chi^2 = 4.9$, df = 1, $p < 0.05$) (Figure 6b). Rainfall was positively correlated with PC1 (Figure 6c)($\chi^2 = 10$, df = 1, $p < 0.005$). We did not find cumulative early season fires to be significantly associated with mid-upper level vegetation density ($\chi^2 = 0.3$, df = 1, $p = 0.6$).

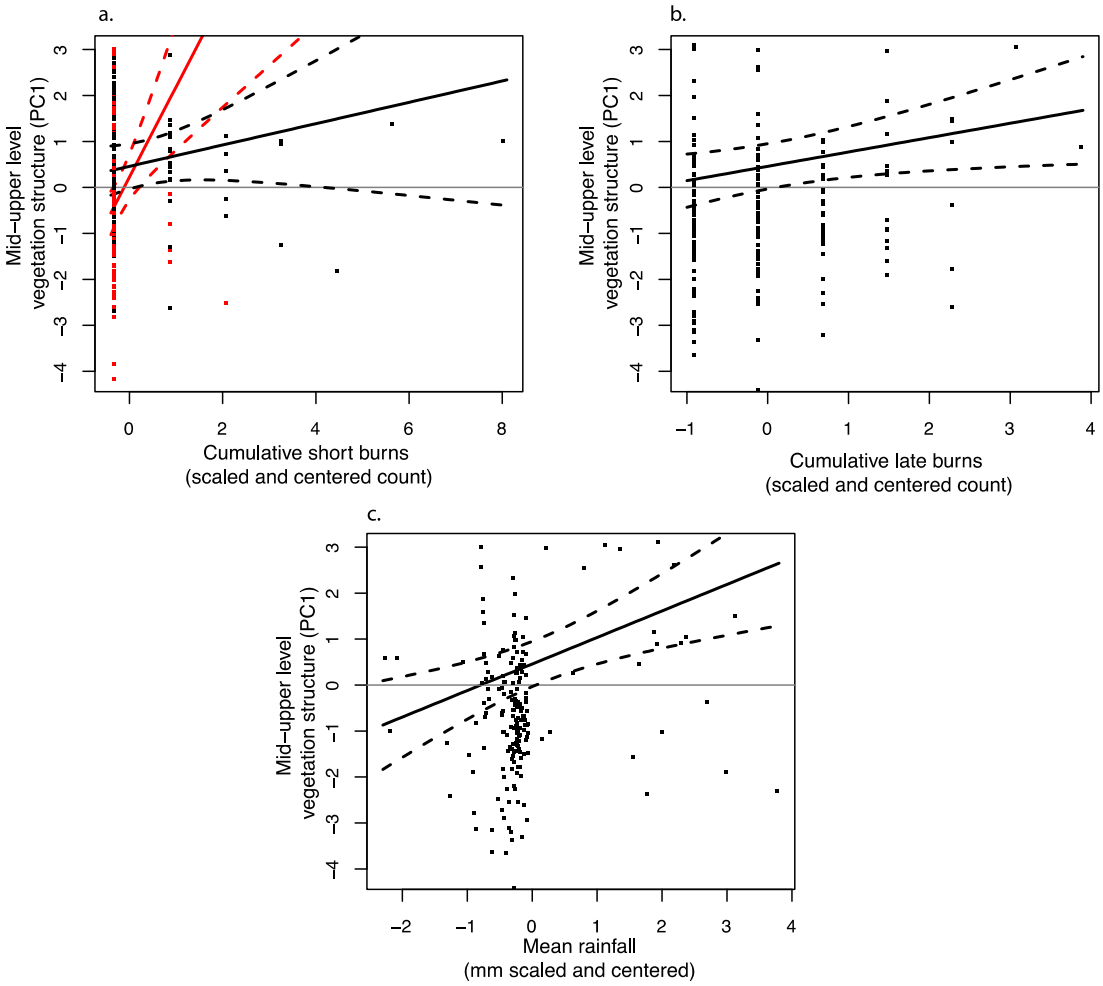

Figure 6 Response of mid-upper level vegetation structure (PC1) to covariates, from the minimum adequate GLS model. Solid and dotted lines represent model predicted values and their respective 95% confidence limits. **a.** Cumulative short fire season burns in sites unburnt for over one calendar year (red) and those experiencing a recent fire event (black). **b.** Cumulative late season burns **c.** Rainfall.

Vegetation effects on bird communities

Vegetation structure parameters (PC1 and PC2) explained a small but significant 3.4% of variance in bird community structure (pseudo-$F_{2,204}$ = 3.6, $p < 0.005$, N.Perm = 199) (Figure 7). Vegetation structure PC1 explained 2.5% of variance in bird community composition (pseudo-$F_{1,205}$ = 5.2, $p < 0.005$, N.Perm = 199), and vegetation structure PC2 explained 0.94% of variance (pseudo-$F_{1,205}$ = 1.9, $p < 0.005$, N.Perm = 199).

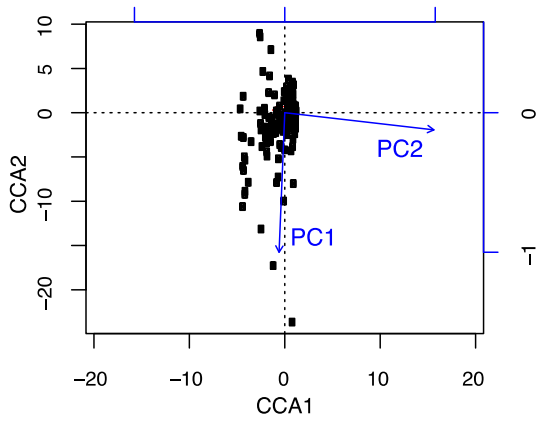

Figure 7 CCA ordination of bird community composition constrained by PC1 (mid-upper level vegetation structure) and PC2 (low level understory vegetation structure).

Responses of bird density and diversity to vegetation structure (PC1 and PC2) were not significant (Appendix 3 Table 1 and 2). Shannon diversity was not significantly correlated with lower level vegetation structure (PC2) (χ^2 = 0.085, df = 1, p = 0.4) or mid-upper level vegetation structure (PC1) (χ^2 = 0.41, df = 1, p = 0.8). Bird density was also not significantly correlated with lower level vegetation structure (PC2) (χ^2 = 1.7, df = 1, p = 0.2) or mid-upper level vegetation structure (PC1) (χ^2 = 0.54, df = 1, p = 0.5).

Discussion

The results broadly supported our prediction that bird community structure, diversity, and density are linked to recent fire history. Research suggests a wide range of variability in bird community dynamics in response to fire, ranging from moderate (Mills 2004), to considerable impacts (Little et al 2013), and acting on different time scales (Woinaski & Recher 1997). Structuring of the bird community composition data by fire parameters suggested that the patterns of occurrence of a recent fire event within one

year, and cumulative fire regimes over the course of 10-15 years do indeed impact birds. Statistically, the ordination structuring and regression trends did not appear particularly strong, but this is largely unsurprising given our broad brush field sampling approach and the coarse resolution of MODIS burned area data and interpolated rainfall and grass nitrogen maps. The suite of rapid sampling techniques for birds and vegetation structure allowed a large area to be sampled in the Serengeti Ecosystem albeit at coarse resolution. The trade-off was an expectedly high variance in raw bird community data and vegetation structure data. Additionally, using MODIS burned area product pixel centroids at 500m resolution introduced error because small fires and partially burned pixels resulted in incorrect classification of the sample sites' fire history. Similarly, the variance of the data and the coarseness of the interpolated maps of rainfall of grass nitrogen limited the effect detectable of even these known bottom-up ecosystem drivers (Sinclair et al 2009).

Repeating the field sampling techniques at multiple sites within each sample pixel would reduce the variation in the field data, and better characterize the bird community and vegetation structure. Similarly, using finer scale fire maps from refined ground-truth dataset available in some areas of the Serengeti would reduce error in fire history classification. Avoiding sampling near natural or man-made fire edges would also limit the error introduced by these firebreaks that occur within a pixel, though accessibility and field safety were a consideration in this study. Given these methodological limitations, detection of statistically weak signals was expected. Nonetheless, the weak statistical significance do reveal effects that suggest biologically meaning influences that support

other results and deserve attention and some of which warrant further finer scaled sampling.

We expected recent fire event occurrence—the variable associated with the immediate temporal impact and post-fire regenerative process—to exhibit strongest structuring of bird community composition. A fire event is projected to change resource availability and directly impact life cycles causing species compositional changes in recently burn areas (Smucker et al 2005, Scott et al 2013). In line with these expectations we found significant differences in bird community structure and diversity (but not density), in response to occurrence of a recent fire event, though the effect was relatively small. We found that in sites not recently burnt, increased nitrogen reduced diversity, but in sites that experienced a recent fire event nitrogen increased diversity. The Shannon index is a composite measure of species richness and evenness. The greater diversity we found in areas that did not experience a recent fire event in the eutrophic southeast may be driven by greater species richness associated with greater complexity in pre-fire habitats (MacArthur & MacArthur 1961). The converse relationship in the dystrophic northwest may be related to evenness. The transient liberation of nutrients after fire (van der Vijver et al 1999) leads to a productivity boom and a consequent temporary increase in functional evenness which promotes species evenness (Mason et al 2005), followed by competition driven reduction in evenness of species abundance over time (Cotgreave & Harvey 1994).

Some of the starkest impacts of fire on birds occur within days and weeks of a fire (Woinarski & Recher 1997). Thereafter, in savannas, post-fire habitats recover rapidly

compared to other fire-prone ecosystems and the effects of even relatively severe grass-fires may be difficult to detect even two months post-fire (Mills 2004). The high-level mobility and rapid response times of birds may limit the ability to detect finer scale impacts. In this study, we effectively combined analysis of immediate impacts and post-burn recovery impacts, but even at the relatively coarse scale of one year we were able to detect significant changes in bird community structure and diversity. In general, our results provide some support for the direct effect of a recent fire event on bird composition and diversity. Indeed, the bird community in this region does adapt to this variability. Further research on mechanisms that affect birds is warranted for example post-fire changes in food resource availability, nesting success, predation risk, and habitat suitability. Additionally, focusing on specific specialists that are less flexible to change may reveal more definitive conservation management implications for those negatively affected (or promoted) by a single fire event.

In general, birds are highly mobile and unlikely to succumb to the direct impact of fire (Lyon and Marzluff 1985, Scott et al 2013), especially in highly fire-prone savanna systems where fire is a frequent occurrence (Mills 2004). Therefore, we expected the community level response not to be primarily attributed to direct effects, but to operate through its indirect effect on vegetation structure (Bond & Keeley 2005, Sankaran 2005, Staver et al 2009). We tested the effects of fire on vegetation structure and found strong evidence that fire, especially a recent fire event, has impacts on vegetation structure, and that birds respond to vegetation structure.

The occurrence of a recent fire event proved to be an important determinant of vegetation structure. This is intuitively evident given the consumption of grass and dry

vegetation by fire, but nonetheless an important result given the predicted response of birds to vegetation structure. Our results suggest that when fire is absent for even one year, increased nitrogen promotes grassy understory growth, but in the year after a fire there is no structural difference between nitrogen rich and nitrogen poor areas. Effectively, a recent fire event results in 'resetting' the grassy understory, after which the effect of nutrients, through their influence on grass composition (Anderson et al 2007a, Hassan et al 2007) and possible interactions with herbivory (Anderson et al 2007b), reestablish the dominant structural pattern of tall grasses in the dystrophic environments and short grasses in eutrophic environments. Birds responded as expected, exhibiting variation in community structure in response to changes in the grassy understory and changes in mid-upper level vegetation structure. This corroborated previous research that highlights the sensitivity of birds to changes in vegetation structure (MacArthur & MacArthur 1961, Skowno & Bond 2003).

In investigating the longer-term effects of fire, we expected bird community structure to change in response to different cumulative burn histories in each fire season. Vegetation structure alteration caused by burning can result in differences in bird community composition (Davis et al 2000), but our study revealed only weak structuring of bird community composition in response to cumulative fire regimes. Overall bird diversity and density were influenced to an extent by cumulative fire regimes. While early season burning was not significantly correlated with either diversity or density, late season burning was associated with a reduction in bird density, but not diversity. Short season fires were positively correlated with density with the strongest effects found in nitrogen rich areas, and in low rainfall areas. However, the interactive effects associated

with short season burns should be treated with some degree of caution as only 20% of the sites had experienced a fire event during in the short fire season, of which only a small fraction were in low rainfall and high nitrogen areas. The strength of these effects certainly warrants further research.

Collectively, the results did not provide strong support for the effect of cumulative seasonal fires on bird composition, density or diversity. This suggests that unlike the avian response following catastrophic fires (Lyon 1997, Baker et al 1997), which may follow a fairly predictable successional recovery (Izhaki & Adar 1997), the impacts are less obvious in frequently burnt African savannas.

We were not entirely surprised by the lack of direct support for long-term fire effects given the indirect mechanism expected to drive the avian response. We expected cumulative fire regimes to impact birds primarily through its effect on habitat alteration (Scott et al 2013). However, our ordination results provide limited support for this prediction, as none of the cumulative fire variables significantly structured vegetation density measures. This is an important result as despite a range of historical burning patterns vegetation structure was not strongly linked to the cumulative seasonal regime parameters. The inverse relationship between fire frequency and fire intensity (Govender et al 2006) may provide a reason for the lack of structuring in the data as the effect of high frequency low intensity fire may result in similar outcomes to low frequency high intensity fires. Infrequent recurrence of fire allows fuel loads to build up resulting in higher intensity fires in contrast to low-intensity frequent burns, where fuel loads have not been allowed to build up. This cancelling effect of intensity and frequency on vegetation structure is not supported by Higgins et al (2007) who confirmed that size

structure and biomass are limited by frequent f ire, a repeated fires can keep individuals small, while large individuals are virtually immune from fire damage. However, our result suggests that a distinct fire regime can lead to multiple habitat outcomes due to the complex interactions between fire, herbivory, nutrients and rainfall (Bond & Keeley 2005).

Further investigation through more statistically powerful multiple regression analysis revealed some significant effects of fire on vegetation structure composites. More frequent late season and short season burning corresponded with sparser, more open mid-upper level structure, compared with denser vegetation in areas that did not experience a fire event in these seasons. This result shows some support for the seasonal fire intensity effect found by Smit et al 2010, and further corroborates Govender et al 2006 findings that fuel moisture is a more important determinant of fire intensity than fuel loads. Smit et al 2010 found that woody vegetation cover was more reduced by long-term exposure to dry-season fires than by wet-season fires. Our result shows a similar seasonal contrast between dry late season burning and wet early season burning, though we found no significance for early season burning on vegetation structure. These subtle relationships supported the hypotheses that a greater number of late and short season fires leads to more open habitats and illustrated the importance of fire seasonality in impacting vegetation structure, to which birds are sensitive. This finding is in line with bird community changes in response to fire found by Valentine et al (2007).

While bird community composition was slightly structured by vegetation, there were no broad patterns of density and diversity associated with vegetation structure. Greater habitat density can be associated with high species diversity and density among

birds (Tews et al 2004). Our results suggested variable bird diversity and density in spite of changes in habitat structure. This may have been because minor habitat alterations change patterns of habitat use as opposed to strong attraction or avoidance of the modified habitats (Lyon & Marzluff 1985). Alternatively, the broad extent of our study in habitats of very different composition and resource availability, may have limited our ability to pick up subtle changes in bird density and diversity within different habitat types.

Although our results did confirm the importance of fire in structuring bird communities, the effects were weaker than we expected. An important reason for this might be key interactive influences of other environmental variables. As a top-down driver, fire effects are not independently deterministic but depend on bottom-up drivers and other top-down drivers (Bond 2005, Archibald et al 2009, Staver et al 2009). In the savanna, rainfall and nitrogen are generally viewed as the major bottom-up drivers that determine to a large extent the spatial and temporal pattern of flammability in the ecosystem (Staver et al 2011). Rainfall in particular is shown on a global scale to be a major determinant of productivity in savannas (Lehmann et al 2014) and has consequently strong influences on fuel loads and fire seasonality (Balfour & Howison 2002). However, our results provided limited support for the structuring of vegetation across the nitrogen and rainfall gradients. We observed a wide degree of variability in grass and tree biomass across the rainfall gradient, highlighting the level of system complexity and suggesting additional unaccounted for drivers, which influence fire through their impact on vegetation. These may include topographic relief, soil, shallow petrocalcic hardpan geology, and herbivory (Sinclair et al 2009).

Although we found statistically significant associations, it is perhaps remarkable how small they are. This low significance reflects the considerable unexplained variance in vegetation structure that may reflect the unknown patterns of herbivory. Herbivory was one of the most important drivers that was not accounted for in this study, due to a lack of adequate data. As another major top-down driver, herbivores compete with fire as they consume what would otherwise become potential fuel for fire (Bond & Keeley 2005). While fire overrides grazing in its direct impacts on birds (Little et al 2013), the indirect influence of herbivory on fire is likely important. Herbivory levels may have confounded our ability to detect the influence of fire. Additional complexity is added by the fact that herbivory in the Serengeti system not only has a spatial component, in conjunction with nutrient availability and habitat structures, but also a cyclic temporal component, since herbivores migrate in response to rainfall and nutrient patterns (Holdo et al 2009a). However, despite the missing explanatory contribution of herbivory the small effects of fire are ecologically reasonable and corroborated by other results.

The lack of strong structuring of vegetation in response to cumulative fire indicates that habitat outcomes remain unpredictable without more information. For example, low incidence of fire was associated dense foliage in some areas, and open foliage in other areas. In effect, the same fire regime defined by minimal fire incidence resulted in two very contrasting habitat types, to which we found birds to be sensitive. The interaction of herbivory and fire may have been a missing link in this scenario, whereby heavy grazing may limit fire occurrence (Archibald et al 2005), or alternatively fire may be limited by high vegetation density (Bond & Parr 2010). Outcomes of the same fire regime may therefore be starkly different. High rates of herbivory and

consequent fire suppression may lead to habitats of low foliage density. In contrast, low herbivory rate and a lack of fire incidence may lead to very denser foliage. Therefore, without accounting for the impact of herbivory we are unable to know the habitat structure outcome associated with few fires.

Lack of structuring in bird community composition in response to fire may also have been linked to fire intensity, a variable only peripherally considered in this study. Fire intensity varies with season and fire frequency changes fuel loads, impacting the severity of fires (Govender et al 2006). In the Serengeti, early fire season is associated with cooler, patchier fires, in contrast to the hot intense fires of the late season (Sinclair et al 2009), but finer resolution analysis of intensity may be critical to bird community response. Our results indicated that more numerous fire occurrences across the time series were not associated with broad changes in tree density. This suggests that low incidence of fire may result in denser foliage in some areas, but minimal fire occurrence may also result in high intensity, habitat-transforming fires in other areas. Therefore minimal fire incidence over the course 15 years could be associated with a wide range in vegetation structure. Other grassland bird studies have shown community level changes in response to fire severity (Smucker et al 2005, Valentine et al 2007). Habitat change as a result of fire can be very different depending on the intensity of fire (Archibald et al 2013). Therefore, investigating the impact of fire intensity within and between early, late, and short season fires may reveal additional impacts.

The effects of short season fires on bird community structure, diversity, density and vegetation could be particularly important, as even the limited evidence provided here suggests that the short burning season may have particularly strong impacts. Short

season burning—a common practice in the Serengeti ecosystem that enables biannual fire occurrence—is a fairly unique phenomenon in African savannas, restricted to regions of high rainfall and bimodal rainfall seasonality (Sinclair et al 2009). Given its local distinctiveness, and apparent strong effects, we recommend further focused research.

The interaction between fire and other variables suggested that the effects of fire are not consistent across the ecosystem. We recommend research on fire impacts specific to narrow ranges of environmental variability. For example, short fire season burns, and to a lesser extent late season burns, are restricted to a high rainfall areas. Contrasting the effect of short season burns across the whole ecosystem may be inappropriate, and instead the effect of short season fires should be investigated within the range of environmental conditions that allow its potential occurrence.

While our findings do not have alarming conservation implications, unlike Mills (2004), we do not agree that the effects of fire are negligible from a management perspective. At the community level, birds appear to be highly resilient to the range of variation in fire regimes in the Serengeti. However, there are many questions that remain unanswered with regard to appropriate fire management for faunal conservation in general (Parr & Chown 2003, Parr & Andersen 2006), and for the distinctive Serengeti context in particular. The community level structuring that we detected suggests that important changes may occur lower levels. The scope of this study did not address specific species or functional group sensitivity to fire. In fire prone systems, fire sensitivity is a conservation concern especially for some functional groups, such as granivorous birds (Franklin et al 2005). For endemic and range restricted species, and highly specialized grassland species more focused research is required. We advised

experimental research in the Serengeti ecosystem to control for the wide range of environmental variability and in particular the missing link of herbivory.

Conclusion

Fire is a major ecosystem process in savannas with important implications for avian ecology and conservation. Despite the high degree of variation in bird community and vegetation structure, our results suggest that both recent fire events and longer-term fire regimes are ecologically influential. Specifically, recent fire events were more important in influencing bird communities than cumulative fire history. Variation in bird community structure, diversity and density was correlated with the immediate impact of fire and post-fire regeneration processes. Cumulative fire regimes were also weakly correlated to bird community structure. The impact of fire on birds acts through alteration on habitat structure, to which birds respond. Short season burning appeared to have significant influences on birds and vegetation structure, and these preliminary findings warrant further investigation. Given the post-fire changes in vegetation and bird community structure, we recommend against burning large expanses on a single day or even in a single season to allow some degree of continuity in the landscape. We also recommend that conservation managers think carefully about the expected habitat change in response to burning and the consequent changes in bird assemblages able to utilize the modified habitat. These decisions need to consider both short-term and to some extent long-term habitat impacts. Further research is required to elucidate the effects of herbivory and fire intensity on bird composition, and we advise focused research on species and functional groups of conservation interest.

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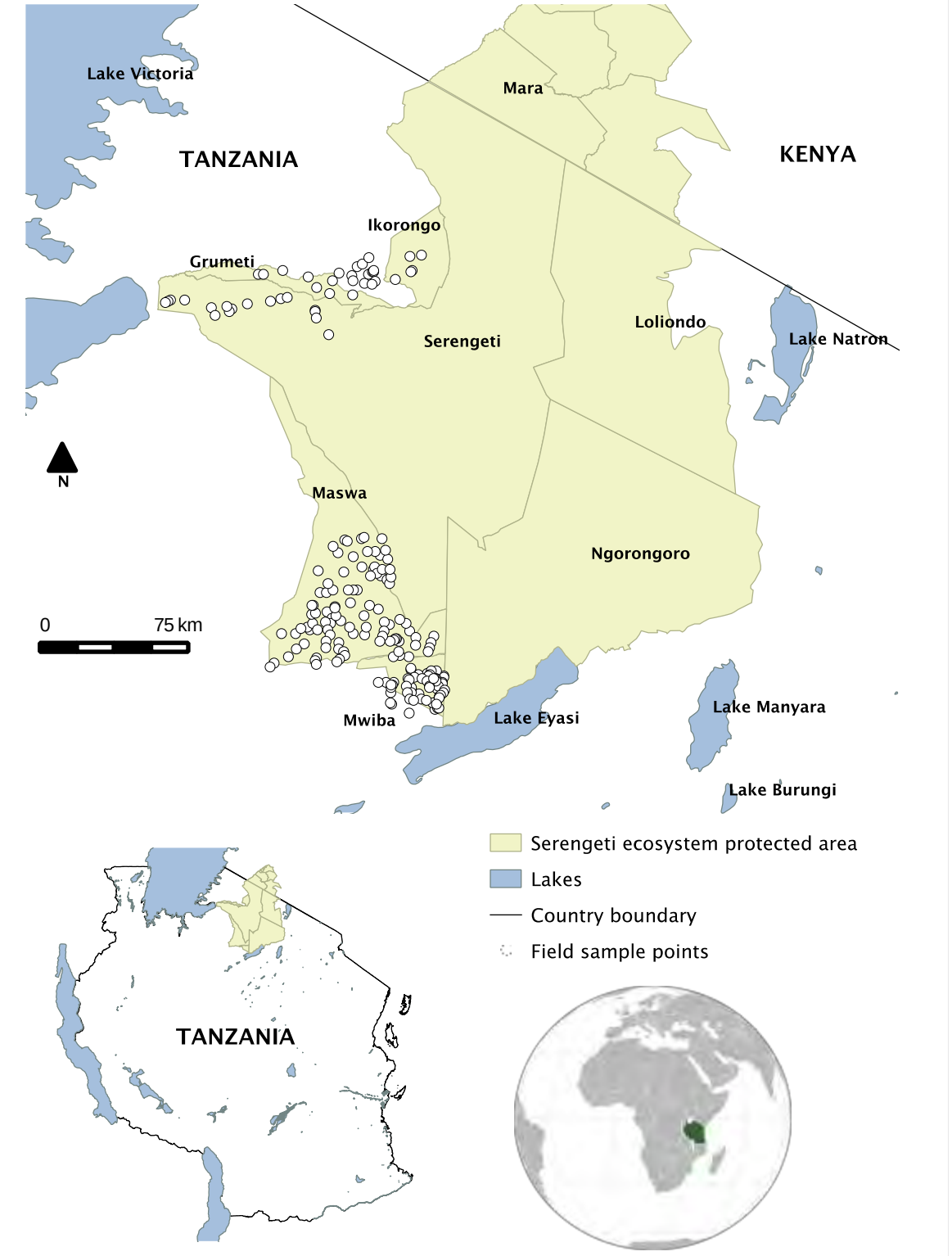
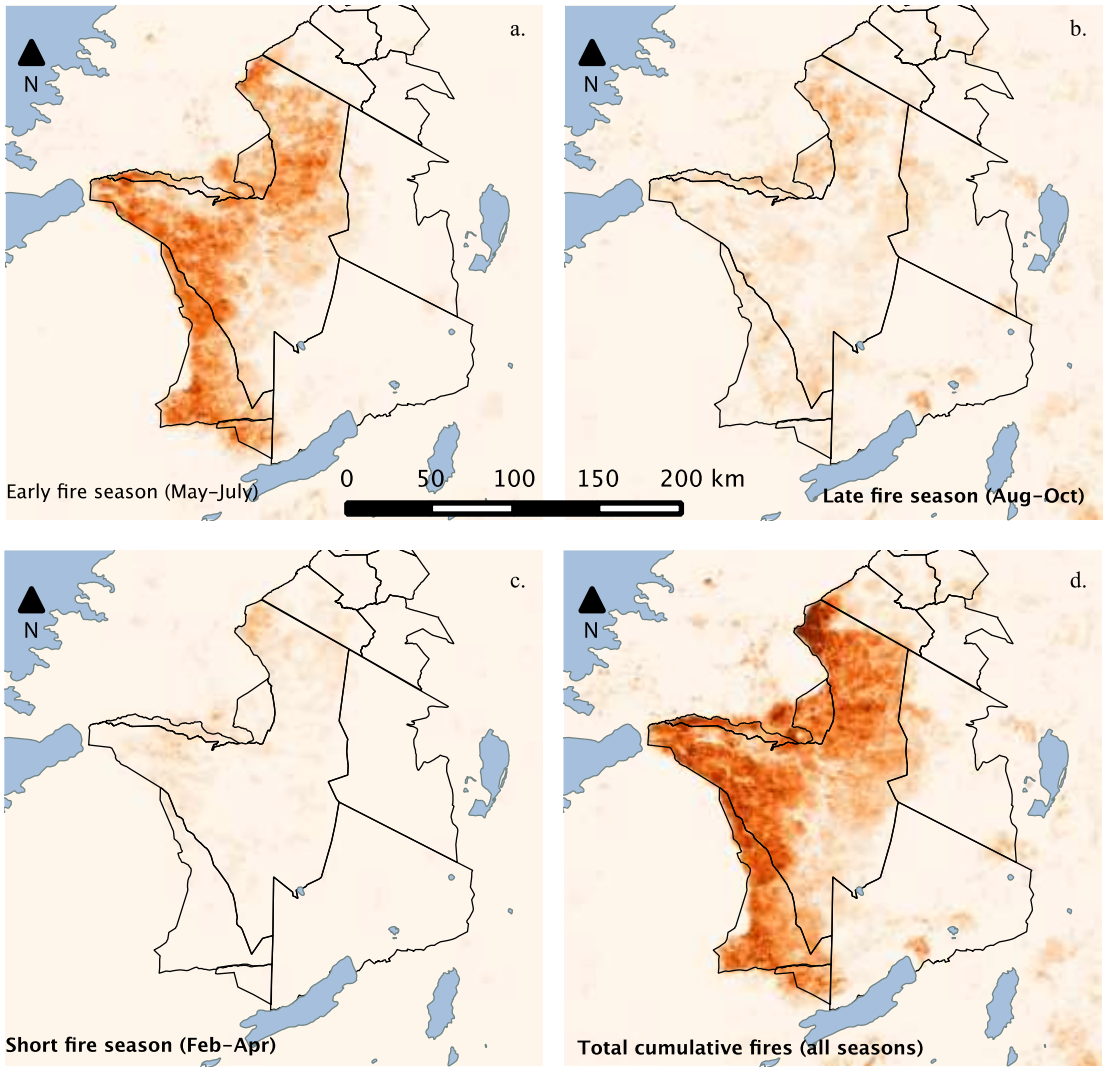
APPENDIX 1: Maps

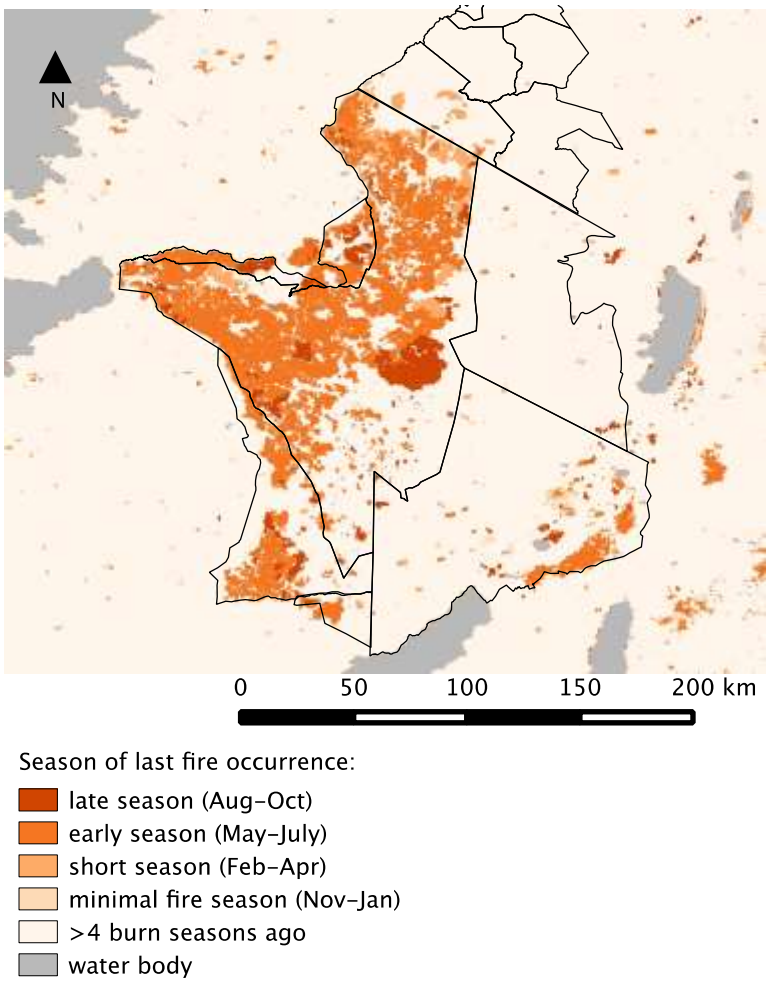


Appendix 1 Map 1 Serengeti ecosystem protected areas in northern Tanzania and southern Kenya, including distribution of field sample points.



Appendix 1 Map 2. Cumulative fire occurrence between January 2000 - October 2013 summarized by fire season:
a. Early burn season in May-July (Julian days 121-212)
b. Late burn season in August-October (Julian days 213-304)
c. Short burn season in February-April (Julian days 32-120)
d. Cumulative burns across all fire seasons for the full time series.
Data from MCD45A1 Moderate Resolution Imaging Spectroradiometer (MODIS) Burned Area product at 500-meter resolution, obtained through the Land Processes Distributed Active Archive Center (LP-DAAC).

Appendix 1 Map 2

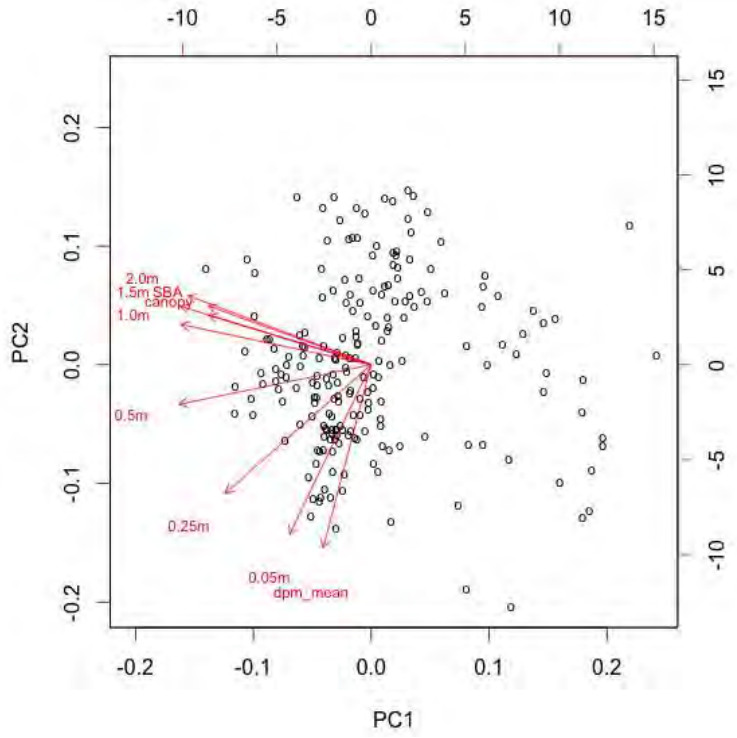


Appendix 1 Map 3 Season of the last fire event within one calendar year (2013), and areas unburnt in the last year.

APPENDIX 2: Data preparation

Appendix 2 Table 1 Eigenvectors for first two principle components (PC1 and PC2) derived from a principle component analysis of vegetation structure measures. These PCs explain 75% of the variance in vegetation structural measures.

Vegetation structure measure	PC1	PC2
DPM_{grass}	-0.10	-0.59
0.05m	-0.17	-0.55
0.25m	-0.31	-0.41
0.5m	-0.40	-0.13
1.0m	-0.40	0.13
1.5m	-0.40	0.19
2.0m	-0.39	0.22
SBA	-0.34	0.19
$Canopy_{max}$	-0.34	0.16



Appendix 2 Figure 1 Plot of first two principle components derived from a principle component analysis of nine structural vegetation measures from sample points in the Serengeti ecosystem. The first two principle components (PC1 and PC2) account for 53% and 22% of the variation respectively. PC2 describes low level understory vegetation structure, and PC1 describes mid-upper level vegetation structure.

Appendix 2 Table 2 Bird species list from 207 10-minute points counts in the Serengeti ecosystem comprising 204 species excluding unidentified records. Data preparation required subsetting common species (contributing >1% total density), and pooling data among five exclusive species groups (with < 45 detections) to fit detection probability functions.

Scientific name	Common name	Common	Grass	Medium	Large	Small	Aerial
Accipiter badius	Shikra				☐		
Accipiter melanolecus	Great Sparrowhawk				☐		
Accipiter minullus	Little Sparrowhawk				☐		
Agapornis fischeri	Fischer's Lovebird	☐				☐	
Alopochen aegyptiacus	Egyptian Goose				☐		
Amadina fasciata	Cut-throat Finch					☐	
Anaplectes rubriceps	Red-headed Weaver			☐			
Anthoscopus caroli	African Penduline Tit					☐	
Anthreptes orientalis	Eastern Violet-backed Sunbird					☐	
Anthus cinnamomeus	Grassland Pipit		☐				
Apalis flavida	Yellow-breasted Apalis	☐					
Apus aequatorialis	Mottled Swift						☐
Apus affinis	Little Swift						☐
Apus apus	Eurasian Swift						☐
Aquila pomarina	Lesser Spotted Eagle				☐		
Aquila rapax	Tawny Eagle				☐		
Aquila verreauxii	Verreaux's Eagle				☐		
Ardea cinerea	Grey Heron				☐		
Ardea melanocephala	Black-headed Heron				☐		
Batis molitor	Chin-spot Batis	☐					
Bradornis microrhynchus	Grey Flycatcher					☐	
Bubalornis niger	Red-billed Buffalo Weaver			☐			
Bubo lacteus	Verreaux's Eagle Owl				☐		
Bubulcus ibis	Cattle Egret				☐		
Bucorvus cafer	Southern Ground Hornbill				☐		
Buphagus africanus	Yellow-billed Oxpecker			☐			
Buphagus erythrorhynchus	Red-billed Oxpecker			☐			
Buteo augur	Augur Buzzard				☐		
Camaroptera brachyura	Grey-backed Camaroptera	☐					
Campephaga flava	Black Cuckoo Shrike			☐			
Campethera nubica	Nubian Woodpecker			☐			
Caprimulgus fossii	Square-tailed Nightjar		☐				
Centropus superciliosus	White-browed Coucal			☐			
Cercotrichas leucophrys	White-browed Scrub Robin	☐					

Scientific name	Common name	Common	Grass	Medium	Large	Small	Aerial
Charadrius asiaticus	Caspian Plover		☐				
Chrysococcyx caprius	Didric Cuckoo			☐			
Cinnyricinclus leucogaster	Violet-backed Starling					☐	
Circaetus cinereus	Brown Snake Eagle				☐		
Circaetus pectoralis	Black-chested Snake Eagle				☐		
Circus pygargus	Montagu's Harrier				☐		
Cisticola aridulus	Desert Cisticola					☐	
Cisticola brunnescens	Pectoral-patch Cisticola					☐	
Cisticola chinianus	Rattling Cisticola	☐					
Cisticola juncidis	Zitting Cisticola					☐	
Cisticola natalensis	Croaking Cisticola					☐	
Clamator glandarius	Great Spotted Cuckoo			☐			
Colius striatus	Speckled Mousebird					☐	
Coracias caudata	Lilac-breasted Roller			☐			
Coracias garrulus	Eurasian Roller			☐			
Corvinella melanoleuca	Magpie Shrike			☐			
Corvus albus	Pied Crow			☐			
Corythaixoides personata	Bare-faced Go-away Bird	☐					
Cosmopsarus unicolor	Ashy Starling	☐		☐			
Cossypha heuglini	White-browed Robin Chat			☐			
Creatophora cinerea	Wattled Starling	☐		☐			
Crinifer zonurus	Eastern Grey Plantain Eater			☐			
Cuculus solitarius	Red-chested Cuckoo			☐			
Cursorius temminckii	Temminck's Courser		☐				
Cypsiurus parvus	Palm Swift						☐
Delichon urbica	House Martin						☐
Dendropicos fuscescens	Cardinal Woodpecker			☐			
Dendropicus goertae	Grey Woodpecker			☐			
Dicrurus adsimilis	Fork-tailed Drongo	☐					
Dinemellia dinemelli	White-headed Buffalo Weaver	☐		☐			
Dryoscopus cubla	Black-backed Puffback			☐			
Emberiza flavivenrtris	Golden-breasted Bunting					☐	
Emberiza tahapisi	Cinnamon Rock Bunting					☐	
Empidornis semipartitus	Silverbird			☐			
Eremomela icteropygialis	Yellow-bellied Eremomela					☐	
Eremopterix leucopareia	Fischer's Sparrow Lark		☐				
Estrilda erythronotus	Black-cheeked Waxbill					☐	
Euplectes capensis	Yellow Bishop			☐			
Eupodotis cafra	White-bellied Bustard				☐		

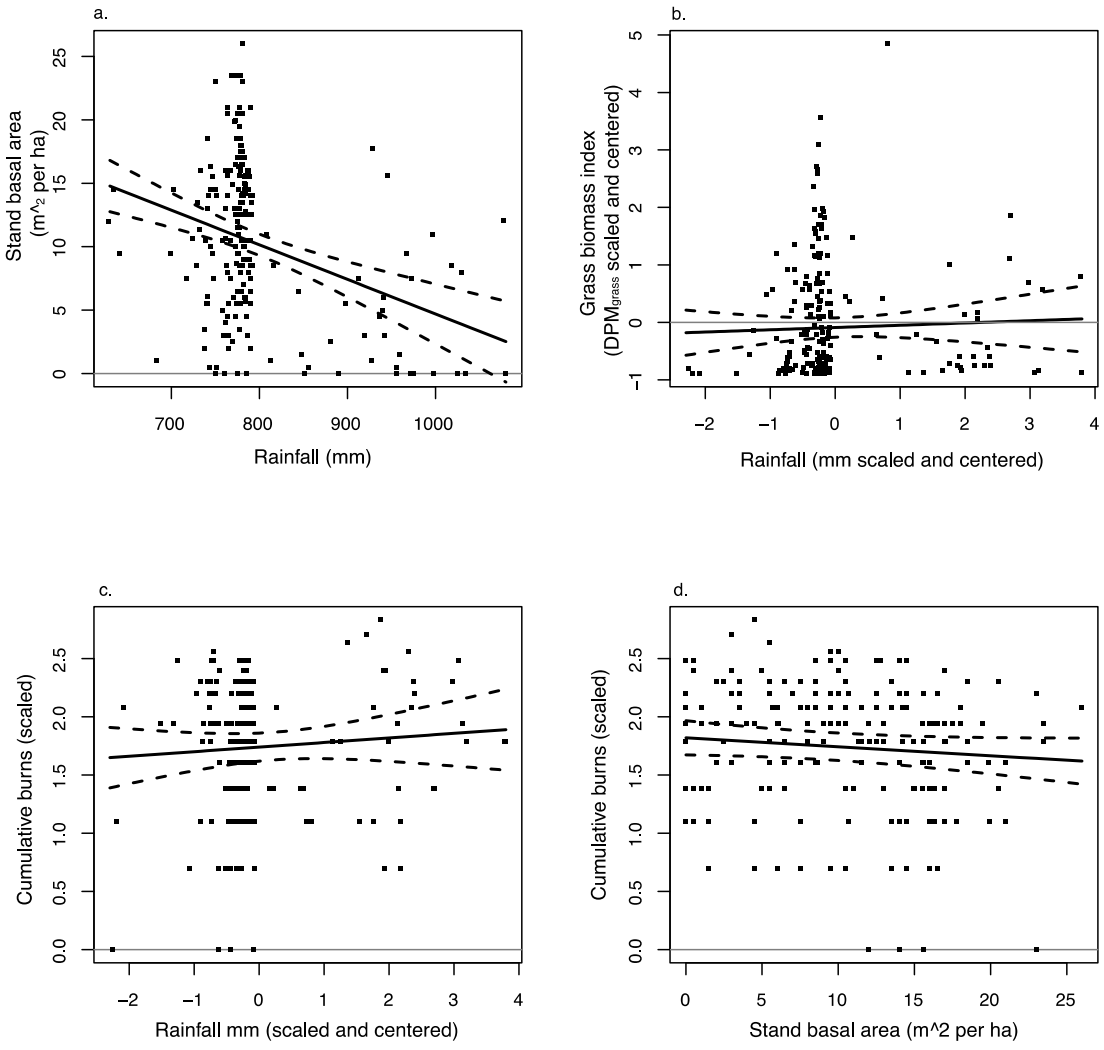
Scientific name	Common name	Common	Grass	Medium	Large	Small	Aerial
Eupodotis melanogaster	Black-bellied Bustard				✓		
Eurocephalus rueppellii	Northern White-crowned Shrike	✓		✓			
Francolinus coqui	Coqui Francolin	✓	✓				
Francolinus rufopictus	Grey-breasted Spurfowl	✓					
Francolinus sephaena	Crested Francolin	✓	✓				
Francolinus shelleyi	Shelley's Francolin		✓				
Gelochelidon nilotica	Gull-billed Tern				✓		
Glaucidium perlatum	Pearl-spotted Owlet			✓			
Gyps africanus	White-backed Vulture				✓		
Gyps rueppellii	Rüppell's Griffon Vulture				✓		
Halcyon albiventris	Brown-hooded Kingfisher			✓			
Halcyon chelicuti	Striped Kingfisher			✓			
Halcyon leucocephala	Grey-headed Kingfisher			✓			
Halcyon senegalensis	Woodland Kingfisher			✓			
Hieraaetus spilogaster	African Hawk Eagle				✓		
Hirundo daurica	Red-rumped Swallow						✓
Hirundo fuligula	African Rock Martin						
Hirundo fuligula	African Rock Martin						✓
Hirundo rustica	Barn Swallow	✓					✓
Hirundo senegalensis	Mosque Swallow						✓
Histurgops ruficauda	Rufous-tailed Weaver		✓				
Indicator indicator	Greater Honeyguide			✓			
Indicator minor	Lesser Honeyguide			✓			
Lagonosticta senegala	Red-billed Firefinch					✓	
Lamprotornis chalybaeus	Blue-eared Starling			✓			
Lamprotornis hildebrandti	Hildebrandt's Starling	✓					
Lamprotornis purpuropterus	Rüppell's Long-tailed Starling	✓					
Lamprotornis superbus	Superb Starling	✓		✓			
Laniarius aethiopicus	Tropical Boubou			✓			
Laniarius funebris	Slate-coloured Boubou	✓					
Lanius excubitorius	Grey-backed Fiscal			✓			
Leptoptilos crumeniferus	Marabou Stork				✓		
Lybius leucocephalus	White-headed Barbet			✓			
Macronyx ameliae	Rosy-breasted Longclaw		✓				
Macronyx croceus	Yellow-throated Longclaw		✓				
Malaconotus sulfureopectus	Sulphur-breasted Bush Shrike						
Melierax metabates	Dark Chanting Goshawk				✓		
Merops apiaster	Eurasian Bee-eater						✓

Scientific name	Common name	Common	Grass	Medium	Large	Small	Aerial
Merops pusillus	Little Bee-eater					✓	
Micronisus gabar	Gabar Goshawk				✓		
Mirafra africana	Rufous-naped Lark		✓				
Mirafra africanoides	Fawn-coloured Lark		✓				
Mirafra rufocinnamomea	Flappet Lark						
Muscicapa striata	Spotted Flycatcher					✓	
Nectarinia kilimensis	Bronze Sunbird					✓	
Nectarinia mariquensis	Mariqua Sunbird					✓	
Nectarinia pulchella	Beautiful Sunbird					✓	
Nectarinia senegalensis	Scarlet-chested Sunbird					✓	
Nectarinia venusta	Variable Sunbird	✓					
Nilaus afer	Brubru	✓					
Numida meleagris	Helmeted Guineafowl	✓	✓				
Oena capensis	Namaqua Dove			✓			
Oenanthe oenanthe	Northern Wheatear			✓			
Oenanthe pileata	Capped Wheatear			✓			
Oenathe pleschanka	Pied Wheatear			✓			
Onychognathus morio	Red-winged Starling			✓			
Oriolus auratus	African Golden Oriole			✓			
Oriolus larvatus	Black-headed Oriole			✓			
Oriolus oriolus	Eurasian Golden Oriole			✓			
Parus albiventris	White-bellied Tit					✓	
Parus fringillinus	Red-throated Tit					✓	
Passer eminibey	Chestnut Sparrow					✓	
Passer rufocinctus	Rufous Sparrow					✓	
Passer suahelicus	Swahili Sparrow	✓				✓	
Petronia pyrgita	Yellow-spotted Petronia			✓			
Phoeniculus minor	Abyssinian Scimitarbill			✓			
Phoeniculus purpureus	Green Wood Hoopoe			✓			
Phylloscopus trochilus	Willow Warbler					✓	
Ploceus intermedius	Lesser Masked Weaver			✓			
Ploceus xanthops	Holub's Golden Weaver			✓			
Pogoniulus pusillus	Red-fronted Tinkerbird					✓	
Poicephalus meyeri	Brown Parrot			✓			
Polemaetus bellicosus	Martial Eagle				✓		
Polihierax semitorquatus	Pygmy Falcon			✓			
Polyboroides radiatus	Gymnogene				✓		
Prinia subflava	Tawny-flanked Prinia					✓	
Prionops poliolophus	Grey-crested Helmet Shrike			✓			

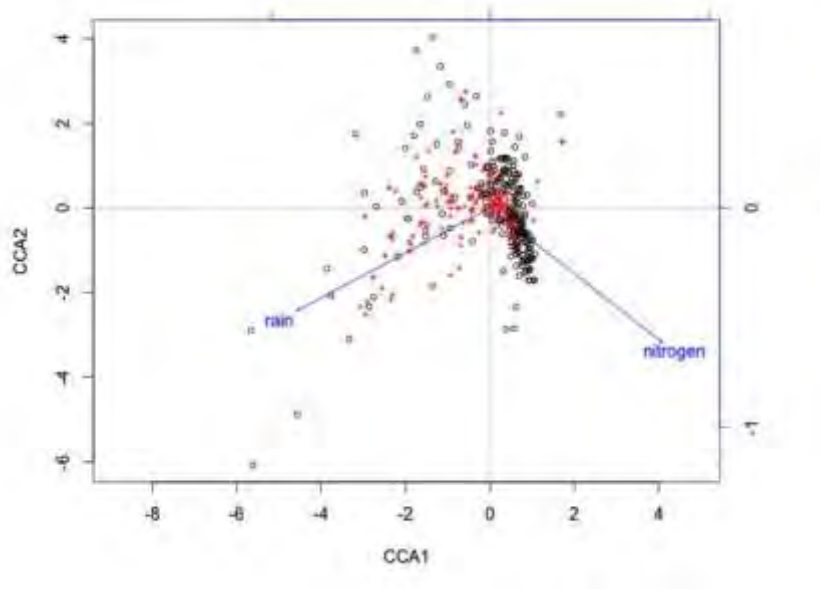
Scientific name	Common name	Common	Grass	Medium	Large	Small	Aerial
Prodotiscus regulus	Wahlberg's Honeybird			✓			
Psalidoprocne albiceps	White-headed Saw-wing						✓
Pseudonigrita arnaudi	Grey-capped Social Weaver					✓	
Pterocles decoratus	Black-faced Sandgrouse		✓				
Pterocles exustus	Chestnut-bellied Sandgrouse		✓				
Pterocles gutturalis	Yellow-throated Sandgrouse		✓				
Pycnonotus barbatus	Yellow-vented Bulbul	✓					
Pytilia melba	Green-winged Pytilia					✓	
Quelea quelea	Red-billed Quelea					✓	
Rhinoptilus africanus	Two-banded Courser		✓				
Riparia cincta	Banded Martin						✓
Schoutedenapus myoptilus	Scarce Swift						✓
Scopus umbretta	Hamerkop				✓		
Serinus dorsostriatus	White-bellied Canary					✓	
Serinus reichenowi	Yellow-rumped Seedeater					✓	
Sporopipes frontalis	Speckle-fronted Weaver					✓	
Streptopelia capicola	Ring-necked Dove	✓					
Streptopelia decipiens	Mourning Dove			✓			
Streptopelia lugens	Dusky Turtle Dove			✓			
Streptopelia semitorquata	Red-eyed Dove			✓			
Streptopelia senegalensis	Laughing Dove			✓			
Struthio camelus	Ostrich				✓		
Sylvia atricapilla	Blackcap					✓	
Sylvia boehmi	Banded Parisoma					✓	
Sylvietta whytii	Red-faced Crombec					✓	
Tchagra australis	Brown-crowned Tchagra	✓					
Tchagra senegala	Black-crowned Tchagra			✓			
Terathopius ecaudatus	Bateleur				✓		
Terpsiphone viridis	Paradise Flycatcher			✓			
Tockus deckeni	Von der Decken's Hornbill	✓					
Tockus nasutus	Grey Hornbill				✓		
Tockus ruahae	Ruaha Hornbill	✓					
Torgos tracheliotus	Lappet-faced Vulture				✓		
Trachyphonus usambiro	Usambiro Barbet			✓			
Treron australis	Green Pigeon			✓			
Tricholaema diadematus	Red-fronted Barbet	✓					
Tricholaema lacrymosus	Spot-flanked Barbet					✓	
Tricholaema melanocephalus	Black-throated Barbet	✓					
Tringa glareola	Wood Sandpiper		✓				

Scientific name	Common name	Common	Grass	Medium	Large	Small	Aerial
Turdoides jardineii	Arrow-marked Babbler			☐			
Turdoides rubiginosus	Rufous Chatterer			☐			
Turdoides sharpei	Black-lored Babbler			☐			
Turnix sylvatica	Button Quail		☐				
Turtur chalcospilos	Emerald-spotted Wood Dove	☐					
Upupa africana	African Hoopoe			☐			
Uraeginthus bengalus	Red-cheeked Cordonbleu					☐	
Uraeginthus cyanocephalus	Blue-capped Cordonbleu					☐	
Uraeginthus ianthinogaster	Purple Grenadier					☐	
Urocolius macrourus	Blue-naped Mousebird					☐	
Vanellus armatus	Blacksmith Plover		☐				
Vanellus coronatus	Crowned Plover		☐				
Vanellus lugubris	Senegal Plover		☐				
Vanellus senegallus	Wattled Plover		☐				
Vidua paradisaea	Eastern Paradise Whydah					☐	

APPENDIX 3: CCA and GLS model results



Appendix 3 Figure 1 Bivariate GLS model results showing the impact of rainfall on **a.** Stand basal area (SBA) ($\chi^2 = 21$, df = 1, $p < 0.0001$), **b.** Grass biomass (DPM_{grass}) ($\chi^2 = 0.27$, df = 1, $p = 0.6$) and **c.** Cumulative burns between 2000-2013 ($\chi^2 = 0.72$, df = 1, $p = 0.4$). **d.** The effect of SBA on cumulative burns ($\chi^2 = 2.5$, df = 1, $p = 0.1$). Solid and dotted lines represent model predicted values and their respective 95% confidence limits.



Appendix 3 Figure 2 CCA ordination of bird community structure constrained by rainfall and nitrogen by species (+) and sample points (o).

Appendix 3 Table 1 GLS model results for response of Shannon diversity, showing sequence of covariate elimination and respective likelihood-ratio test statistics and p-values from multiple regressions toward the minimum adequate model: Shannon diversity ~ short burns + nitrogen + last fire + rain + short burns : nitrogen + nitrogen : last fire

Variable	Coefficient	Standard Error	LRT (1d.f.)	p-value
vegetation structure PC1			0.041	0.8
late burns:last fire			0.089	0.8
last fire: rain			0.20	0.7
vegetation structure PC2			0.85	0.4
nitrogen:rain			0.79	0.4
short burns:rain			0.38	0.5
early burns:nitrogen			1.7	0.2
early burns:last fire			0.85	0.4
late burns:rain			3.1	0.1
late burns:nitrogen			1.5	0.2
late burns			1.6	0.2
short burns:last fire			3.3	0.07
early burns:rain			2.3	0.1
early burns			0.039	0.8
rain	-0.13	0.036	13	0.0002
short burns:nitrogen	0.16	0.045	13	0.0002
nitrogen:last fire	0.22	0.073	9.6	0.002
short burns	0.22	0.088		
nitrogen	-0.14	0.061		
last fire	0.061	0.067		
Intercept	2.5	0.053		

Appendix 3 Table 2 GLS model results for response of bird density, showing sequence of covariate elimination and respective likelihood-ratio test statistics and p-values from multiple regressions toward the minimum adequate model: Bird density ~ late burns + short burns + rain + short burns:rain

Variable	Coefficient	Standard Error	LRT (1d.f.)	p-value
last fire:rain			0.0019	0.97
late burns:nitrogen			0.0062	0.9
nitrogen:last fire			0.0096	0.9
late burns:last fire			0.0079	0.9
early burns:last fire			0.18	0.7
early burns:nitrogen			0.12	0.7
late burns:rain			0.057	0.8
vegetation structure PC1			0.54	0.5
vegetation structure PC2			1.7	0.2
nitrogen:rain			2.5	0.1
short burns:nitrogen			0.72	0.4
nitrogen			0.60	0.4
early burns:rain			2.5	0.1
early burns			2.8	0.09
short burns:last fire			3.7	0.05
last fire			3.4	0.07
late burns	-2.9	1.4	4.1	0.04
short burns:rain	-4.2	1.8	5.2	0.02
short burns	8.2	3.3		
rain	0.057	1.7		
Intercept	67	1.8		

Appendix 3 Table 3 CCA results for analysis of raw vegetation structure measures constrained by cumulative fire for each of three fire seasons: early, late, and short. Ordination structuring was not significant (N.Perm =99).

Constraining variable	Accounted variance (%)	pseudo-$F_{1,205}$	p-value
Early	0.64	1.3	0.4
Late	0.12	0.25	0.9
Short	0.60	1.3	0.3
Rainfall	0.80	1.7	0.2
Nitrogen	0.80	1.8	0.2

Appendix 3 Table 4 GLS model results for response of vegetation structure PC2, showing sequence of covariate elimination and respective likelihood-ratio test statistics and p-values from multiple regressions toward the minimum adequate model: Vegetation structure PC2 ~ nitrogen + last fire + rain + nitrogen : last fire + nitrogen : rain

Variable	Coefficient	Standard Error	LRT (1d.f.)	p-value
early burns:nitrogen			0.0033	1.0
last fire:rain			0.0045	0.9
short burns:last fire			0.021	0.9
late burns:nitrogen			0.030	0.9
late burns:rain			0.026	0.9
short burns:nitrogen			0.36	0.5
early burns:rain			0.84	0.4
early burns:rain			0.84	0.4
early burns:last fire			1.1	0.3
early burns			0.039	0.8
short burns:rain			1.5	0.2
short burns			0.42	0.5
late burns:last fire			2.1	0.1
late burns			0.0040	0.95
nitrogen:last fire	0.58	0.20	8.2	0.004
nitrogen:rain	-0.36	0.13	7.4	0.01
nitrogen	-0.22	0.17		
last fire	-1.0	0.20		
rain	-0.65	0.16		
Intercept	0.39	0.17		

Appendix 3 Table 5 GLS model results for response of vegetation structure PC1, showing sequence of covariate elimination and respective likelihood-ratio test statistic and p-value for multiple regressions toward the minimum adequate model: Vegetation structure PC1 ~ late burns + short burns + last fire + rain + short burns : last fire

Variable	Coefficient	Standard Error	LRT (1d.f.)	p-value
early burns:last fire			0.13	0.7
late burns:rain			0.18	0.7
late burns:nitrogen			0.12	0.7
short burns:rain			0.24	0.6
early burns:rain			0.40	0.5
last fire:rain			0.23	0.6
late burns:last fire			0.45	0.5
short burns:nitrogen			1.4	0.2
nitrogen:last fire			2.1	0.1
early burns:nitrogen			1.2	0.3
early burns			0.30	0.6
nitrogen:rain			2.7	0.1
nitrogen			2.9	0.09
late burns	-0.23	0.33	4.9	0.03
rain	0.58	0.18	10	0.002
short burns:last fire	1.7	0.55	9.9	0.002
short burns	0.23	0.18		
last fire	-0.23	0.33		
Intercept	0.46	0.25		